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Effects of Light on Plants

A Literature Review, 1950

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PREFACE

This comprehensive summary review of publications on light effects on plant growth and development was written by the late W. W. Garner in 1950. It is published with only very minor editorial changes from a manuscript which he left, to record a contribution by one of the two pioneers who discovered photoperiodism. It gives his interpretation on problems of light relationships to plant response, particularly photoperiodism in 1950, after a lifetime of research in this field. He discusses the role of visible and near-visible radiation and reviews the literature on effects of light duration, intensity and quality in relation to growth and physiologic process of plants, phototropism, phytosynthesis, and photoperiodism.

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Prepared in

Crops Research Division
Agricultural Research Service
U.S. Department of Agriculture

EFFECTS OF LIGHT ON PLANTS
A LITERATURE REVIEW, 1950

By W. W. Garner[1]

VISIBLE AND NEAR-VISIBLE RADIATION

Sunlight

Primary source of radiant energy for plant life is the sun. The term, sunlight, in its generally accepted meaning, refers to the whole of the incoming solar radiation rather than to just the portion of it to which the human eye responds, which constitutes true light.

Sunlight as it reaches the earth's surface at sea level is made up of a continuous series of wavelengths of radiant energy ranging from about 285 to 2,400 millimicrons (mu). The shorter wavelengths--up to about 390 mu--form what is known as ultraviolet radiation, while wavelengths that extend from 390 to about 760 mu constitute the visible portion of the spectrum, and the longer wavelengths from 760 up to approximately 2,400 mu supply infrared radiation. While the color of light is a function of wavelength or quality, the limits of the wavelength bands assignable to the six colors in the visible spectrum cannot be defined precisely. However, the ranges in wavelengths usually allocated to the primary colors are, in millimicrons, approximately: Violet, 390 to 430; blue, 430 to 490; green, 490 to 550; yellow, 550 to 590; orange, 590 to 640; red, 640 to 760.

At the top of the earth's atmosphere the average annual energy value of radiation from the sun, commonly known as the solar constant, is about 1.94 gram calories per square centimeter per minute (g. cal. per $cm.^2$ per min.). Before reaching the earth's surface, however, the radiation is considerably modified in both intensity and quality by action of the air and its ever-changing content of water vapor, dust, smoke, and other constituents (47)[2]. Moreover, as a result of the scattering action of the air and its impurities and the modifying effects of clouds on the incoming solar radiation, a variable but important part of it arrives in the form of diffuse light so that ordinary daylight is made up partly of direct sunlight and partly of skylight.

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[1] Deceased.

[2] Figures (underscored) in parentheses refer to Literature Cited at the end of this publication.

Daylight Variability

Extreme variability is one outstanding characteristic of daylight. The voluminous observational data available show that many variables are involved. At noon, on a clear day, at sea level, the skylight accounts for as much as 15 percent or more of the total solar radiation received on a horizontal surface. Just after sunrise and just before sunset its energy value, although low on an absolute basis, actually exceeds that of direct sunlight. Skylight is richer in shorter light rays than direct sunlight. However, in dealing with effects of sunlight on plant growth consideration usually is given only to the combined energy values of the diffused- and the direct-light fractions.

In any searching analysis of light effects on plant growth and development, consideration must be given to each of the three factors or elements of the light complex, namely, (1) intensity, (2) quality or wavelength, and (3) daily duration. Under certain exceptional conditions quantity of illumination may function as a unit factor, in that increase in intensity may fully compensate decrease in duration, or increase in duration may fully offset decrease in intensity. Again, in growth movement phenomena, direction of incident light has definite effects, but usually these effects are regarded as involving essentially unequal illumination intensities on opposite sides of the plant or plant organ. Comprehensive data are found in publications of the Smithsonian Institution, of the United States Weather Bureau, and of corresponding institutions in foreign lands showing average values and ranges of variation and other characteristics applying to each of the three factors (47, 50, 75, 87).

Subject to possible disturbing effects of fluctuating weather conditions, the intensity and quality of sunlight at any particular location vary from sunrise to sunset each day, in accordance with definite schedules. In like manner, subject to the effects of uncertain weather conditions, the intensity and daily duration and, to a lesser degree, the quality of light vary with the time of year and the latitude in definite, orderly fashion. Again, intensity and spectral composition of daylight vary with the altitude. Finally, local surface conditions, such as uneven topography and plant formations, may strongly influence illumination values.

At Washington, D. C., in June the total daily solar radiation on a horizontal surface averages about 540 g. cal. per cm.^{2} per min., while in midwinter it drops to about 150 g. cal. per cm.^{2} per min. (50). For the higher, drier regions of the West the radiation values are somewhat higher. The maximum intensity ordinarily reached at noon on a clear day at sea level on a horizontal surface is about 1.5 g. cal. per cm.^{2} per min., but for average sky in June the noon intensity at sea level approximates 1 g. cal. per cm.^{2} per min. The luminous equivalent of 1 g. cal. per cm.^{2} per min. of daylight averages 6,700 foot-candles although the relationship between the luminous values and the caloric energy varies somewhat with the elevation of the sun (87). With respect to the quality of daylight, the energy content of the ultraviolet component is relatively low, averaging not more than 2 to 3 percent of the total radiation. Although the peak of the energy distribution curve of daylight normally occurs at about 500 mu, in the blue-green region of the visible spectrum, the infrared radiation supplies about 55 percent of the total. Accordingly, the visible portion of the daylight spectrum constitutes somewhat less than 45 percent of the total energy.

The factor of direction of the incoming sunlight, which normally involves unequal illumination of opposite sides of the exposed plant, relates primarily to the apparent daily course of the sun across the sky from approximately east to west. Duration of daylight, from sunrise to sunset--one of the most striking and significant variables of the daylight complex--involves a marked interrelationship of seasonal and latitudinal conditions. Beginning with a fixed day length of 12'7" at the equator, the maximum and minimum durations on June 21 and December 22, respectively, change with increase in latitude as follows: at 20°, 13'20" and 10'55"; at 40°, 15'1" and 9'19"; at 60°, 18'52" and 5'32". Above the Arctic Circle (66°30') daylight is continuous for at least a portion of the summer and night is continuous for at least a portion of the winter. The annual range in length of day at Washington, D. C., latitude 39°, is shown graphically in figure 1.

Sources of Artificial Light

Although the ever changing character of sunlight affects plant life as a whole, obviously it is not a suitable source of illumination for conducting quantitative studies in the effects of light on plants, where constant condition is required. Progress in effective use of artificial illumination in plant research studies has been hampered by lack of suitable light sources.

In most latitudes the daily light period is too short during the winter months for growth and development of many plants. Although great strides in artificial lighting have been made, as yet sunlight has not been successfully reproduced.

The arc lamp perhaps was the first form of artificial light to be used in growing plants. In improved form, it is still employed, but its spectrum is deficient in the longer wavelengths of light. Because of its simplicity in operation, the tungsten filament lamp has been most widely used. But its spectrum contains a marked excess of red and infrared radiation, which under some conditions may be injurious to plants (11). The fluorescent lamp produces a spectrum which, as a whole, rather closely resembles that of daylight although it is deficient in the dark red rays and differs somewhat in other particulars from natural light (179). The fluorescent lamp and the arc lamp, with improved carbons or supplemented with incandescent filament lamps, appear to be fairly well suited to growing plants in artificial climates under constant, controlled conditions (129). It is well to remember, however, that it may prove difficult to apply the

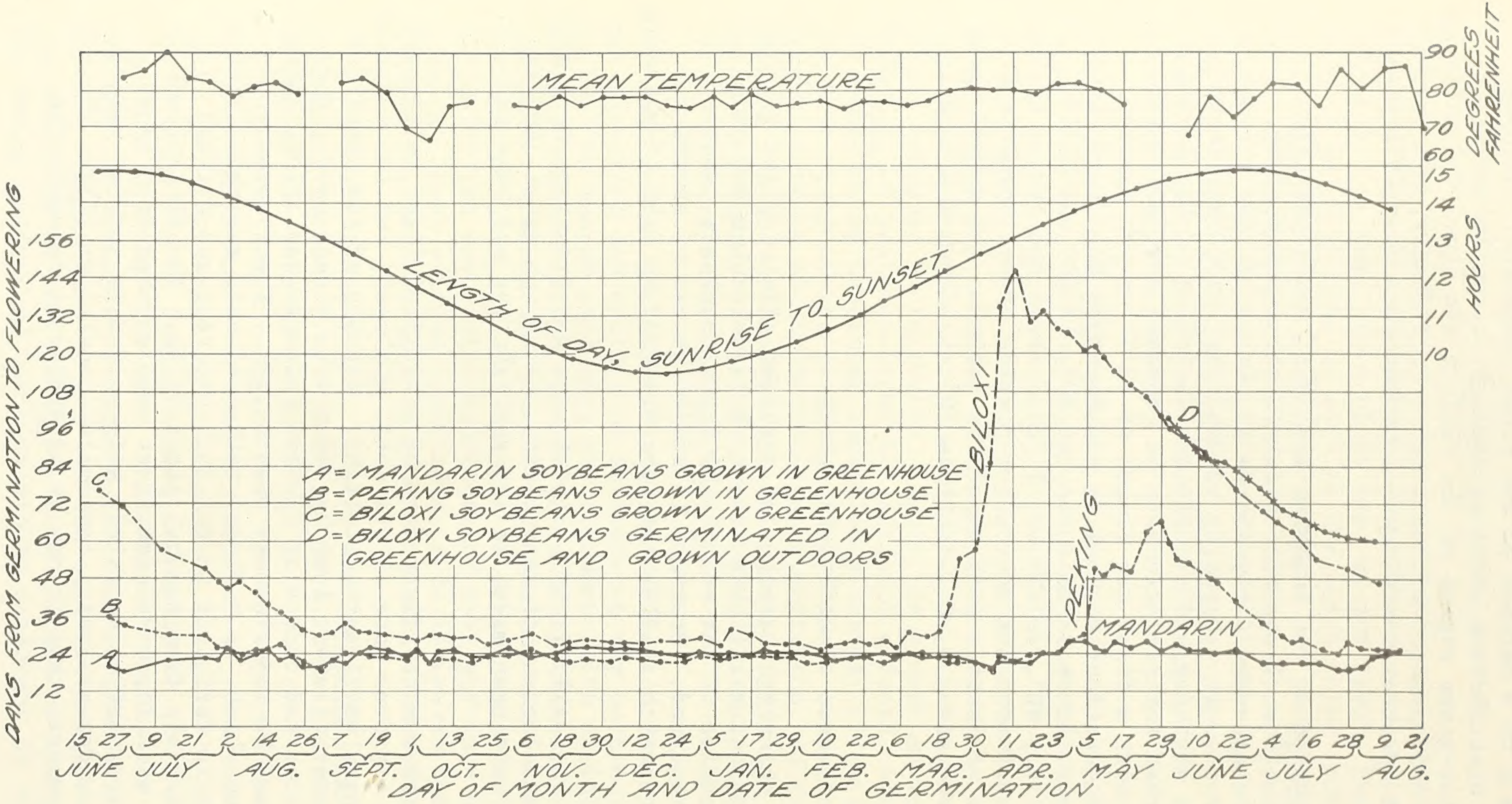

Figure 1.--Duration of the vegetative period in plantings of early, medium, and late soybean varieties made at short intervals throughout a period of 14 months at Washington, D. C. With a favorable, comparatively constant mean temperature, all varieties flowered in less than 30 days when germination took place during the short days of fall, winter, and early spring. In response to the increasing photoperiod of late spring, however, plantings of the late variety, Biloxi, changed over to early-fall flowering, and 6 weeks later the medium variety, Peking, likewise changed over to late-summer flowering. (See Literature Cited 63.)

results obtained under either rigidly fixed or abruptly changing conditions directly to plant life in the open, where usual normal diurnal changes in light conditions are gradual rather than abrupt. When artificial illumination is employed only to supplement daylight as a means of controlling the daily light period, the requirements are much less exacting, provided the basal illumination is adequate. Here, the tungsten filament lamp is often satisfactory. In some cases neon light also can be used at night as a supplement to solar radiation (143).

LIGHT INTENSITY AND QUALITY IN RELATION TO GROWTH AND PHYSIOLOGIC PROCESSES OF PLANTS

In dealing with the effects of light on growth and related physiologic processes of the plant, it is important to keep in mind that these effects represent the combined action of the intensity, the quality, and the daily duration of the radiation to which the plant is exposed. In other words, the response of the plant to any one of these elements of the light factor is subject to modification through interaction of the others. For example, the comparative effects on plant growth of different wavelengths of light cannot be interpreted satisfactorily without considering the intensities of radiant energy received by the plant and the duration of the irradiation.

The effect of various features of plant growth and related internal physical and chemical processes as affected by light intensity and quality pertain chiefly, although by no means exclusively, to the vegetative phase of development. The outline of available information on light-growth reaction and growth substances, one of the most prominent features of plant research in recent years, naturally will include consideration of the factor of direction of light or unilateral illumination in relation to growth movements. In the case of photosynthesis, there are numerous comprehensive surveys of the voluminous literature, some of which are quite recent, so that it does not seem necessary to present here a detailed review of the research in this field.

The effects of daily duration of light on plant growth and development (photoperiodism) is considered in some detail, chiefly because of its intimate bearing on the physiology of flowering while, at the same time, it also may strongly influence practically all features of growth. The discussion of effects of this element of the light factor on plant processes will include comment on its interrelations with intensity, quality, and quantity of light. Literature covering the entire subject of light effects on growth and development of the plant, and the various associated physiological processes, up to about 1936 was surveyed comprehensively by Burkholder (28) and by Duggar and associates (44).

Seed Germination

Extensive observations extending through the past century and a half indicate that in somewhat more than one-half of all plant species, germination of the seeds and fruits in the freshly developed stage is benefited more or less by exposure to light. Light is indispensable for germination in few species, it inhibits germination in many species, and it produces no effect in numerous others.

On relations of light in germination, much confusion developed in the literature, especially in earlier works on the subject, because several other factors, either internal or external, may substitute effectively for light in promoting germination, and thus eliminate the need for light. For example, seeds of certain tobacco varieties and some other species require light when freshly matured and require no light after undergoing a period of after-ripening (140). Alternating of relatively high and low temperatures may accomplish the same result. Kinzel (88) classified an extensive list of plant species with respect to sensitivity of the seed to light. Little is known as to the photochemical processes concerned in the stimulating or inhibiting effects of light on the germination of seeds. The literature in this field was surveyed by Crocker (38).

Plant Growth in Darkness

The effects on growth of alternating darkness and light are discussed in section on photoperiodism. In continuous darkness the duration and extent of growth necessarily depends in large measure on the quantity of food reserves originally present in the seed or storage organ, since there can be no net gain in dry matter content in the absence of light. Plants grown in the complete absence of light develop a distinctive appearance known as etiolation.

An extensive study of growth and development in a large number of plant species maintained in continuous darkness was conducted by MacDougal (101), who also presented a comprehensive survey of the literature up to 1903. Typical features of growth in etiolated plants as observed by MacDougal and subsequently by many others include the production of very tall, weak stems, with long internodes, and poor root development. In dicotyledons no leaves develop, while monocotyledons form very narrow and thin leaves. There is no formation of chlorophyll in most cases and the etiolated tissues show a lesser degree of differentiation than the normal. The plants have a relatively higher content of water. Flower formation occurred in some plants studied, but in all cases the stamens and pistils failed to attain functional maturity (MacDougal 101). Leopold (96) found that Alaska peas and red kidney beans formed flower primordia when propagated in darkness and Irish Cobbler potatoes formed numerous blossoms that were unable to open. Suzuki (159) showed that plants can utilize nitrate to form asparagine in the dark. It is apparent, also, that proteins can be synthesized in plant tissues that receive no light. Many botanists, however, believe that formation of amino acids is especially rapid in the green parts of the plant in the presence of light, perhaps in intimate association with photosynthesis (29). In explanation of the phenomenon of etiolation, MacDougal (101) concluded that light exercises a controlling morphogenic influence on plants, although the mode of action remains rather obscure. With respect to growth, there is evidence that seedlings are able to form limited quantities of auxin, or growth-promoting substance, in the absence of light, probably from the seed reserves. It seems possible that the auxin could become a controlling factor in stem elongation. Jehrén and Went (81) found that squash plants usually live only 4 to 5 days when placed in darkness; but, if a sucrose solution is injected into their hollow petioles, the stems continue to elongate for as long as 30 days. The leaves, however, failed to enlarge significantly even when nucleic and amino acids were injected with the sugar and only strong light stimulated further expansion.

Influence of Intensity of Illumination

Plants must carry on their activities while exposed each day to an extremely wide range in light intensity from dawn till nightfall, while this normal range is often drastically modified for varying periods by changing sky conditions. This situation makes it rather difficult to accurately analyze the light-intensity growth factor--although it is highly important--especially from an ecological standpoint (151). There are two typical developments when etiolated plants are exposed to either weak or moderately intense illumination; (1) the foliage leaves rapidly expand and (2) the plants promptly develop a green color. These effects may be produced by extremely small quantities of light. In most other effects, light intensity becomes quite important although there is an extremely wide range in the optimum intensities of various plant species. At relatively very low light intensity growth characteristics closely resemble those observed in continued darkness except for the expanding leaves and the greening of the exposed plant parts. The leaves are relatively large but thin and "sappy" and their tissues are not fully differentiated. In general, stem elongation, length of internodes, and leaf area vary inversely with light intensity, while stem diameter and leaf thickness vary directly with light intensity, especially during early stages of growth (132).

In most sun plants, total growth, as measured by increase in dry matter, increases with increase in the light energy up to about one-fourth to one-half the full daylight intensity. This result is due chiefly to the favorable action of comparatively high illumination intensity on photosynthesis under conditions of natural alternation of day and night. In plant nutrition studies, Davis and Hoagland (40) found that larger yields are produced by light of moderate intensity acting over a longer daily period than by light of high intensity acting for a shorter daily period. High intensity illumination favors increased fruitfulness of plants and usually produces definitely thickened leaves of reduced area, with dense internal structure and comparatively increased development of mechanical and vascular elements.

It has been ascertained that light of sufficient intensity may induce hardening against cold injury and promote drought resistance in perennials. Apparently the increased light intensities normally prevailing in clear skies of the tropics are of comparatively little advantage to vegetation as a whole, because the full daylight intensity is not required for maximum growth. Whether adequate photosynthesis is possible seems to be the chief determining factor in survival of vegetation beneath forest canopies, because light intensity may fall as low as 1 foot-candle or less. Increasing light intensity is commonly linked with rising temperature. It has been found that in some plants at least, the optimum intensity for increase in dry matter increases through a considerable range with increase in temperature. Literature up to 1936 dealing with the effects of light intensity upon seed plants has been critically surveyed by Shirley (150). Shirley (151) also twice reported on the status of research on light as an ecological factor.

Effects of Light Quality

The relative effectiveness of the longer and shorter rays of the visible spectrum and of the ultraviolet and infrared radiation has been a prominent feature of research on phototropism and various phases of light-growth reaction, in photosynthesis, and in photoperiodism. In practically all of the earlier work on light quality in relation to plant growth and development, means for applying radiation of known wavelength and adequate energy content were lacking so that it is difficult or impossible to interpret the results obtained. Even today accurate observational data in this field are limited. There was some evidence even before the 1900's that plants exposed only to the red end of the visible spectrum grew as if exposed to very weak light and early conclusions to that effect seem to have been verified. Popp (133) grew various plants under a combination of open-mesh shade cloth and Corning glass filters of known selective transmission characteristics, using sunlight as the source of illumination. The energy values under the several filters, however, were not equalized. When wavelengths shorter than 529 mu were excluded, in general, abnormal stem elongation occurred. The soybeans, for example, tended to produce vines. In all cases the stems, with few branches, were relatively thin and weak. The leaf and stem tissues were poorly differentiated. The water content of the plants was high while the production of dry matter was reduced. Elimination of only wavelengths below 472 mu produced much the same effects except that they were not so marked. Removal of the ultraviolet radiation alone did not produce these effects. Similar results have been reported by others.

It is evident that growth follows much the same pattern in the absence of the blue-violet rays as in very weak white light or continuous darkness. Abnormal elongation of the stems under these conditions is due chiefly to increased cell elongation. In absence of the longer wavelengths of light, on the other hand, the blue end of the spectrum tends to produce a sturdy but more or less stunted type of growth. There is ample evidence to show that plants grow best with radiation containing all wavelengths of the visible spectrum. It is well to keep in mind, moreover, that to insure "normal" plant growth and development the energy distribution of the light source should closely conform to that of sunlight.

Popp and Brown (134) made a critical review of the earlier work relating to influence of ultraviolet radiation on plants. The evidence in this field as a whole indicates that wavelengths shorter than 290 mu produce decidedly harmful effects. However, in any event, this component of solar radiation is absorbed by the atmosphere and so does not reach the earth's surface. There seems to be no satisfactory evidence that the ultraviolet radiation of wavelengths above 290 mu, which may be present in sunlight, has any important beneficial action on plant life. Absorption of the near infrared wavelengths up to 800 to 900 mu is relatively low but increases decidedly with further increase in wavelength. Although the infrared constitutes upward of 50 percent of the total energy of sunlight, it is not generally effective in dry-weight production. It may be distinctly harmful when present in excess, as in some forms of artificial light, especially under conditions of limited water supply. The importance of taking into consideration the infrared component in dealing with the effects of visible radiation on plants has been pointed out by Johnston (83).

Transpiration and the Absorption of Minerals

Sunlight has long been known to have marked effect in increasing transpiration in plants due to the large quantity of the radiant energy absorbed by the leaves and to the action of light in causing the stomata to open. The action of light in transpiration was emphasized by the classical studies of Brown and Escombe (24) which served to demonstrate the surprisingly high efficiency of the stomatal apparatus for outward and inward gaseous diffusion.

It has been generally considered that light brings about opening of the stomata chiefly by lowering the hydrogen-ion concentration in the guard cells, which in turn, operates in some way to modify the osmotic concentration within the cells and consequently, their turgor. With respect to the mechanism involved, several investigators have held that the reduced acidity favors increased conversion of the starch usually present in the guard cells into sugars. Alvim (6) presented evidence tending to show that phosphorylase is the enzyme concerned in shifting the starch-sugar equilibrium and thereby changing the osmotic conditions in the cells. The evaporation of water from the plant's surfaces is influenced by various external and internal factors, some of which interfere considerably with efforts to clearly evaluate the light effects. Numerous investigators, however, have shown that transpiration increases with increase in light intensity. Thus, Martin (107) found that in Helianthus, transpiration varied directly with the illumination intensity up to full midday sunlight. It has been observed, however, that a reduced water supply may result in closing of the stomata even in the light, thereby checking transpiration. Apparently all wavelengths of the visible spectrum are effective in regulating stomatal movements.

Arthur and Stewart (10) showed that at moderate temperatures, transpiration of tobacco plants was much reduced under infrared radiation exposure as compared with the effects of white light, whereas at higher temperatures the water loss under the infrared approached that in the visible spectrum, even though the stomata were closed. Hoagland and associates (80) found that actively growing roots can readily absorb ions against a concentration gradient provided the plant receives adequate illumination for producing the carbohydrate needed by the roots as a source of energy. To the extent that light increases transpiration it may be said to promote rapid movement of absorbed ions to the various plant parts. Considerable evidence indicates that streaming of cytoplasm in active cells is accelerated by light and experimentally the red end of the spectrum has been observed to produce maximum effects. This action of light on protoplasm deserves mention here in that many years ago the theory was advanced that rotational streaming of protoplasm in the sieve tube elements of the phloem supplied an effective medium for transport of solutes. According to some authorities, however, this phenomenon does not ordinarily occur in mature sieve tube elements except in water plants. As observed in younger tissues, the rate of movement is too slow to be effective in the translocation of solutes.

Formation of Chlorophyll and Other Pigments

Plants apparently need a variety of pigments for effective absorption of the radiant energy utilized by them. Moreover, light is indispensable for the formation of some pigments of the plant. Nearly all autotrophic plants, including some of the photosynthesizing purple and green bacteria, contain chlorophyll, carotene, and xanthophyll. Most red and blue-green algae also contain photosynthetically active proteinaceous pigments known collectively as phycobilins. Each of these four types of pigments occur in numerous modifications. In most of the higher plants, except the conifers, light is essential to the development of chlorophyll from a precursor, protochlorophyll, the synthesis of which apparently is not dependent upon light. In the higher plants, chlorophyll occurs only in the chloroplasts. It is always accompanied by carotene and xanthophyll, and these pigments readily absorb blue radiation, although their true function in the economy of the plant has not been fully elucidated. There is evidence, however, that they participate in light-growth reaction. Xanthophylls and, perhaps, carotenes, are also present in etiolated plants. They commonly persist, moreover, after the chlorophyll disappears in aging leaves and in some ripening fruits.

The chlorophyll content required for adequate photosynthetic activity varies widely in different species. Ordinarily on a dry-weight basis plants grown in shade contain a higher percentage of chlorophyll than those grown in sun. Light of high intensity tends to decompose chlorophyll as well as to synthesize it, so that above a certain relatively low level the content of chlorophyll varies inversely with the light intensity. According to Sayre (144), all wavelengths of radiation from 300 up to 680 mu are more or less effective in the synthesis of chlorophyll, while extreme red and infrared radiation does not promote the process.

The most effective regions of the spectrum in the formation of chlorophyll are essentially those most active in photosynthesis. There is some evidence that a combination of the shorter and longer wavelengths gives best results. Observations by Rabideau et al. (138) and Seybold and Weissweiler (148) on the optical properties of foliage leaves have shown that in the normal green leaf maximum absorption of visible radiation takes place at 660 to 680 mu, which is the maximum chlorophyll absorption band. Minimum absorption occurs at 540 to 560 mu and a second high absorption rate, at about 450 mu. The green leaf absorbs nearly all of the incident ultraviolet remaining in solar radiation as it reaches the earth's surface and likewise a large proportion of the infrared component.

The carotenoids are widely distributed in yellow flowers, fruits, and leaves and in many seeds. The occurrence of these pigments in roots, as in carrots, shows that their formation does not depend directly upon light, but that illumination may increase the carotenoid content of aerial plant parts. It has been shown that the blue end of the spectrum is more effieient than the red in the formation of carotene and xanthophyll. Van Niel (167) reviewed the status of research up to 1943 on the development and functions of the chloroplast pigments.

Numerous anthocyanins and related pigments dissolved in the cell sap are responsible for most of the red, blue, and purple colors of flowers and fruits, many colors of the autumn leaves, the reds of cabbage and beet roots, and the yellows of certain flowers and other plant parts. According to several authorities, formation of red pigment in certain apple varieties results from the action of the blue, violet, and ultraviolet portions of sunlight. In fact, there seems to be general agreement that these regions of the spectrum are the most effective in the formation of anthocyanins. Various proposals have been advanced as to functions of the anthocyanin group of plant pigments, but there is little direct evidence in support of any of them. The monograph of Onslow (123) contains lists of organs of many plant in which formation of anthocyanin pigments takes place in the dark and others in which pigment development seems to be dependent upon light. Arthur (8) has surveyed the literature up to 1936 on effects of radiant energy on anthocyanin pigments in plants.

In view of the enormous proportions of the photosynthetic activities of aquatics in the oceans and inland waters, the light relations of their pigments are of considerable interest. The depths at which submerged algae and other water plants are able to thrive in either fresh or sea water may be controlled primarily by the absorptive action of the water on the incident sunlight. Since the blue-green rays are absorbed much less effectively than the red-yellows, both the intensity and the quality of the light may become important factors. Obviously, the intensity at a given depth must be sufficient to enable any particular species growing there to meet its minimum photosynthetic needs if the plant is to survive. At increasing depths, moreover, high efficiency in absorption and utilization by the plant of the blue-green radiation becomes more and more essential for survival. Numerous investigators have concluded that, in general, the submerged algae can absorb and utilize most effectively the wavelengths of light that are complementary to the dominant color pattern of their pigments. Thus, it is thought the blue-green wavelengths are most effective for the red algae, while conversely, red wavelength is most effective for the blue-green algae. Considerable evidence has been developed in support of this relationship, known as chromatic adaption, although not all students of the subject are convinced of its ecological importance. The fact that red algae are found at relatively great depths seems to be in accord with the concept.

PHOTOTROPISM, LIGHT-GROWTH REACTION AND GROWTH SUBSTANCES

Extensive quantitative observations on light intensity and wavelength relations in phototropic phenomena were made by Blaauw (15) within the period, 1909-1919. During and immediately following this period, other investigators carried out detailed studies dealing with light-growth reaction, which seemed to point to the presence in the plant of specific substances capable of regulating various types of growth. As evidence favoring this view rapidly accumulated, this soon became a field of intensive research, and a voluminous literature developed on both the theoretical and the applied aspects of the subject. The coleoptile of the oat plant proved to be especially well adapted to study of the problems involved and has been widely used not only in investigations concerned with phototropic phenomena and light-growth reaction, but also in detailed studies relating to the formation, distribution, and functioning of growth substances in the plant, thus closely linking the research on the three problems. A series of comprehensive reviews and monographs covering the field in part or as a whole appeared from time to time (22, 30, 85, 124, 125, 175, 176).

In his fundamental studies in phototropism, Blaauw sought to explain growth reaction on the basis of direct response to light intensity and quality. With the carbon arc as a light source, he found that the most effective part of the spectrum in inducing growth curvature lies between 466 and 478 mu and the yellow-red portion proved to be inactive. Blaauw considered that the direct action of light is to check growth and so, growth curvature resulting from unilateral illumination is due essentially to a reduced rate of growth on the directly illuminated side of the stem (coleoptile). An exceedingly small quantity of illumination was found to be capable of inducing phototropic activity in the *Avena* coleoptile. Some years later Johnston (84) checked Blaauw's results by means of a special type of monochromator. He found that for the *Avena* coleoptile the phototropic sensitivity curve rises sharply from 410 mu to a maximum at about 457.5 mu, with a second maximum at 470 to 480 mu, followed by a rapid drop toward a threshhold level at about 546 mu.

It seems to be fully established that only the blue end of the visible spectrum is concerned to an important degree in phototropic phenomena. At the same time, there is convincing evidence that the immediate effect of white light is to check the growth rate, as was maintained by Blaauw, although perhaps by a mechanism not contemplated by him. The conclusion seems justified that, regardless of the mechanism concerned, positive phototropic curvature resulting from unilateral illumination is due, at least in part, to the action of the direct light in reducing the growth rate on the illuminated side. However, in 1928 Went (173) published his classical paper which seemed to lead to a different conclusion. He demonstrated that when the tips are cut from Avena coleoptiles and set upright on small blocks of agar for a time and these agar blocks then placed on the cut surfaces of the decapitated coleoptiles, these soon show renewal of active growth at a rate suggestive of the original. Again, it was shown that after the coleoptile has been decapitated, and an agar block containing the exudate from the tip then placed on only one side of the cut surface, growth is soon stimulated in the coleoptile tissues below the agar, resulting in negative curvature in the stump. It is evident, therefore, that a substance or substances capable of regulating growth readily diffuse from the tip into the agar and back again into the coleoptile tissues.

Went (173) showed that under rigidly standardized conditions the degree of curvature of the coleoptile obtained in the last-mentioned test constituted a reliable measure of the quantity of the growth-promoting substance in the agar. This is still the principal method for quantitative analysis of growth substances or auxins. However, other procedures, such as measuring straight growth in sections of coleoptiles, or etiolated pea epicotyls placed in aqueous media containing the growth substance, are also used. Methods for extraction of growth substances from plant material with organic solvents have also been developed. Although voluminous experimental data has been published on the role of growth substances in both tropistic and straight light-growth reaction, much of the material seemingly is contradictory. Consequently, additional work will be required to fully determine the role and mode of action of growth substances in plant growth and development. It has been well established that light plays an important role in the distribution and functioning of the auxins or plant hormones within the plant. In the Avena coleoptile, cell division ceases after the earlier stages of growth so that the growth-stimulating action of auxin ordinarily seen in phototropic response relates only to cell elongation and not to cell division.

Went found that the tip of the coleoptile responds differently than the basal portion to blue light, the former being much more sensitive but reacting less rapidly than the latter. Numerous investigators have concluded that in young dicotyledonous plants auxin is formed chiefly, if not exclusively, in apical plant parts, such as terminal buds, very young leaves, and tips of coleoptiles. Consequently, auxin occurs in highest concentration in those parts. It has been shown that formation of auxin in the terminal buds is most rapid during the grand growth period of the plant, although production in the leaves is largely limited to the earlier stages of their growth. In contrast with these findings, applying to dicotyledons in the younger stages of growth, it appears that in Gingko biloba L. and other woody plants, along with some monocotyledons, the major source of the auxin found in the shoot is not the apical meristem or the leaves but the stem itself (70). Maximum accumulation of the auxin may occur in the internodes near the base of the shoot.

Went carried out experiments which tended to show that when the tip of the Avena coleoptile is exposed to unilateral illumination a portion of the growth substance migrates from the lighted to the shaded side of the tip. Similar results were reported by Boysen-Jensen (22). It has been considered by many, therefore, that the positive curvature resulting from unilateral illumination of the coleoptile is caused largely by greater elongation of the tissue cells on the shaded side which, in turn, is attributed to increased accumulation of growth substance on that side. At the present it is difficult to say whether phototropism in Avena is chiefly due to increased cell elongation on the shaded side or decreased cell elongation on the illuminated side. In any event, differences in auxin concentration in the tissues of the two sides appear to be a major factor in the growth curvature, although it may well be that others are involved.

While formation of growth substances may be stimulated in some instances by light, the maximum accelerating action on growth is exerted in the darkness. Some years ago it was shown that light, even if only of moderate intensity, can in some way inactivate these substances. It has been maintained by some that β-carotene functions as the absorbing pigment in the auxin-inactivating effect of light since the absorption spectrum of β-carotene is similar to the spectral sensitivity curve for phototropism in the Avena coleoptile. It has been shown to be present in the etiolated coleoptile. Evidence has been found, moreover, that this pigment can sensitize the light-inactivation of auxin a. Quite recently, Galston and Baker (56) have found that the yellow vitamin, riboflavin, is widely distributed in the Avena coleoptile and can readily bring about photoinactivation of its diffusible auxin. The absorption spectrum of riboflavin, like that of β-carotene, is similar to the action spectrum for phototropism. Galston and Baker concluded that phototropic response of the basal portion of Avena coleoptile probably is the result of riboflavin-sensitized destruction of auxin.

It is generally agreed that auxin may be present in plants in three forms: (1) bound auxin, which can be extracted with organic solvents; (2) free, diffusible auxin, formerly known as heteroauxin; (3) precursor, convertible into auxin by an enzymatic system (174). It now appears that the diffusible, as well as the extractable auxin of stems, is mainly indoleacetic acid (91). Except for phototropic phenomena, the role of auxin in the extremely varied morphogenetic effects of light on plants presents some very puzzling problems. Normally, transport of auxin is strictly polar and it moves downward from the apical structures through living tissues at a relatively rapid rate. Although auxin is believed to be essential for stem elongation, one of its outstanding effects as it travels downward is its inhibiting action on the development of the lateral buds of the stem.

Thimann and Skoog (161) showed that when exogenous auxin is applied at frequent intervals to the top of the stem after removal of the terminal bud, dormancy of lateral buds is maintained effectively. It also inhibits root elongation. As yet, no satisfactory explanation has been offered as to how auxin produced in shoot tips and other apical structures actively promotes growth in apical buds, especially in darkness, but at the same time inhibits development of axillary buds. In contrast with its inhibiting action on elongation of roots, auxin, along with numerous other auxinlike exogenous substances, is capable of initiating root formation on stems--now a matter of practical importance.

Growth regulators also now have various other important practical applications such as the production of fruits of normal size containing no seeds, the use of sprays or dusts to control fruit drop, the use as herbicides, and for other purposes (111). One of the impressive features of the growth regulator development is the variety of external substances that are capable of producing most, if not all, of the typical growth effects of the endogenous auxins. Even various amino acids have been found to produce profound morphologic effects under continuous light (156).

While the vitamins, which often may function as growth substances, are readily synthesized by the higher plants in at least some of their organs, comparatively little is known about light relations in the formation and functioning of these substances within the plant. The fact that the aboveground plant parts must supply the thiamin or B_1, and possibly several other vitamins required by roots for their normal growth, suggests that light may be involved in the formation and distribution of these growth substances. Reference has been made already to proposals that β-carotene, precursor of vitamin A, and riboflavin, or B_2, may sensitize the photoinactivation of auxin a or of indoleacetic acid. Riboflavin occurs in plants mostly as a component of numerous yellow flavoproteins, which are believed to function as oxidation-reduction enzymes in respiration. It has been suggested that these, as well as riboflavin in the free state, may be activated by light (54, 55). Various enzymes, including the hydrolytic type, may be inactivated by intense light, the blue end of the spectrum being most active, while ultraviolet radiation is especially effective in the process.

PHOTOSYNTHESIS

Extensive early literature relating to photosynthesis in its numerous aspects has been critically surveyed by Stiles (157) and by Spoehr (153). Spoehr and Smith (154) dealt specifically with the light factor. Comprehensive surveys of the field were published by Rabinowitch (139) and by Franck and Loomis (48). Frank and Loomis (48) gave special attention to the mechanism and quantum efficiency of the photosynthetic process.

Among the earliest students of the gas exchange in green plants were Priestley in 1771, Ingen-Housz in 1779, Senebier in 1782, and DeSaussure in 1804. These investigators all found that when exposed to light green plants absorb carbon dioxide and evolve approximately an equal volume of oxygen and that the plants gain in weight as a result of the process. Boussingault from 1860 to 1881 did much toward putting the gas exchange on an exact quantitative basis, but Sachs in 1882 apparently was the first to clearly set forth the fundamental significance of the photosynthetic process. The next outstanding advance came with the brilliant researches of Willstätter and associates (177) which established the chemical composition and structure of chlorophyll and the associated carotinoid pigments of the chloroplast. It was found that typically, the green plant contains two distinct chlorophylls: chlorophyll a, blue-green in solution and having the elementary composition, $C_{55}H_{72}O_5N_4Mg$; chlorophyll b, green in solution and having the composition, $C_{55}H_{70}O_6N_4Mg$. Two yellow pigments also were isolated and identified: carotene, $C_{40}H_{56}$, forming orange-yellow crystals; xanthophyll, $C_{40}H_{56}O_2$, forming yellow crystals. Through the ensuing years there has been an ever-increasing interest in various phases of photosynthesis but, despite the best efforts of biochemists through all of this period, the details of the process whereby the plant converts the elements of water and carbon dioxide into carbohydrate remain among nature's best kept secrets.

Light intensity relations in photosynthesis are complex because of the vagaries of the weather, the regular diurnal and seasonal variations in intensity, and the marked variations due to topography and other local conditions. There are, also, profound differences between plant species in their light requirements. For example, it is stated that Elodea requires light intensity of 12,000 foot-candles for maximum photosynthetic output (66) but Chlorella pyrenoidosa (119) requires considerably less than 1 percent of this intensity for maximum growth. Some forms of marine algae apparently are able to make effective use of moonlight. There is an important time factor in the direct influence of light intensity and other limiting factors on the photosynthetic process, which is not necessarily related to the daily light period. It is now known that increases in the photosynthetic rate associated with increases in light intensity over short periods of time, when an increase above the normal in other factors that may be limiting such as carbon dioxide concentration, often do not correctly reflect ultimate results over prolonged periods (37).

In systematic observations made through the growing season under field conditions at Logan, Utah, Thomas and Hill (162) found that in alfalfa and wheat the course of the photosynthetic curve was controlled mainly by light intensity on both clear and cloudy days. The peak of the curve for alfalfa corresponded to the maximum light intensity on cloudy days but on clear days was reached at a level of intensity well below the maximum.

Böhning (17) obtained continuous records on fully expanded, attached leaves of apples exposed to uninterrupted illumination for various periods up to 18 days. Comparison was made with leaves that had developed under high light intensity and others grown under low intensity illumination.

Under continuous light of 3,700 foot-candles intensity, the rate of apparent photosynthesis of the "sun leaves" remained relatively uniform for a period of 18 days, but with a light intensity of 5,800 foot-candles the rate declined about 40 percent in 14 days. When the "shade leaves" were exposed to continuous light of 3,800 foot-candles, a decided decrease in synthetic activity developed during the first 2 days. After 10 days, a further decline developed. Bleaching of the chlorophyll under prolonged exposure to high light intensity is suggested as the cause of the decline in photosynthetic activity. Available data on the effects of light intensity on photosynthesis under open-air conditions are limited, but for many sun plants intensities of 25 to 50 percent of full daylight appear adequate for maximum efficiency (168). The lower limits of light intensity for survival of many shade plants, as beneath the forest canopy, apparently do not extend much below 5 percent of full daylight, but for others may be far lower.

Although the green color of leaves shows that absorption of the green rays is less intense than that of the longer and shorter wavelengths of light, recent investigations have made it clear that the absorption of green light is greater than was formerly believed to occur (138, 148). It frequently amounts to 60 to 80 percent of the total reaching the leaf surface. It has long been known that in the process of photosynthesis the red end of the solar spectrum is more effective than the blue end. It is also well known, that the red end has a higher energy value. When the energy values applying to all wavelengths of the energy incident upon the plant are accurately balanced, apparently the shorter wavelengths of red light are the most efficient, the blue wavelengths somewhat less so, and the green rays the least efficient. Data reported by several investigators indicate that with absorption of equal quantities of radiation by the leaf, green light is somewhat less effective than red light, but more effective than the blue. With respect to energy actually absorbed by the photosynthetically active pigments, the available evidence indicates that, at most, differences in quantum efficiency of the longer and shorter wavelengths of light are comparatively small (45, 112, 170).

Concerning the mechanism of carbon fixation, there is no general agreement, as yet, as to the first end product or products of the process. Perhaps to most students a hexose sugar has appeared to be the most logical product. It has been recently suggested (29, 119), however, that overall photosynthesis really may include reduction of nitrate and assimilation of the nitrogen, with resultant formation of a series of more complex "end products." The intermediate products in the formation of carbohydrate is still obscure, because at present no substances definitely known to be true intermediates have been isolated and chemically identified. Nearly a century ago formaldehyde was suggested as the initial product formed, but convincing evidence is still lacking in support of this concept.

One of the most significant developments is the accumulation of evidence indicating that all of the oxygen evolved in photosynthesis comes from photolysis of water rather than from reduction of carbon dioxide (86). The hydrogen formed in this way apparently serves to reduce carbon dioxide, perhaps in a series of steps. These findings are based essentially on the use of water or carbon dioxide containing known proportions of radioactive or tracer oxygen, hydrogen or carbon, in connection with photosynthetic gas-exchange studies of the usual type. Moreover, it has been shown by Hill and several later workers (21) that isolated chloroplasts or even aqueous suspensions of chlorophyll and cytoplasmic residues freed from cells and plastids readily cause evolution of oxygen. There is no significant fixation of carbon, however, under these conditions. Although photoreactions play an essenital role in photosynthesis it appears that other reactions are involved, which take place in the dark, and are catalyzed by enzymes. It is now rather generally held that since three quanta of light are required to supply approximately the energy needed for reducing a molecule of carbon dioxide there must be at least three or four separate steps in the photoreduction process and possibly a like number of dark reactions.

During the past decade isotopes of carbon, especially the long-lived C^{14}, have been extensively used in the form of carbon dioxide in renewed efforts to trace the metabolic transformations of carbon compounds from the absorption of the carbon dioxide to incorporating the assimilated products into the structures of the plant. These studies have dealt with carbon fixation and metabolism as a direct result of photosynthesis and, likewise, fixation taking place in the absence of light. As yet, however, the work in this field still leaves open the problem of the actual mechanism of photosynthesis. Research on the subject, with special reference to the results obtained with tracer carbon, has been reviewed by Benson and Calvin (14). Since carbon dioxide fixation readily takes place in organic constituents of various plant and animal organisms by a primary carboxylation reaction in the absence of light, some investigators have suggested that the first stage in the reduction of carbon dioxide is a dark reaction. There is considerable evidence, however, against this theory. While there is general agreement that chlorophyll plays an indispensable role in photosynthesis there is no experimental evidence to indicate that the carotenoid pigments function in the process, even though they invariably accompany chlorophyll in the chloroplasts. In studies with indoleacetic acid and several other growth substances, Freeland (49) observed that most of these depressed the rate of apparent photosynthesis in bean plants.

Impressive results have been obtained in researches dealing with the quantum efficiency of photosynthesis. For most of the work in this field two species of green algae, Chlorella pyrenoidosa and Scenedesmus obliquus, have been used as experimental material. In 1923 Warburg and Negelein (170) found that under favorable conditions only 4 or 5 quanta of red light when absorbed by chlorophyll in green plant cells were required for production of one molecule of oxygen, which indicates an efficiency as high as 65 percent. Subsequently, several other groups of investigators arrived at considerably lower efficiency values (48), centering chiefly around 20 to 25 percent and signifying that at least 10 to 12 quanta of red light are required to liberate a molecule of oxygen or to reduce a molecule of carbon dioxide.

Burk and associates (27), by applying improved and simplified procedures, appear to have fully verified the original findings of Warburg and have extended them in certain directions. These authors concluded that a maximum of 4 quanta of light of wavelengths 630 to 660 mu is required to liberate one molecule of oxygen. Apparently the respiration process was not affected by light of the intensity used in the work.

Precise information concerning the possible influence of light upon plant respiration is indispensable for the accurate evaluation of observational data bearing on photosynthetic efficiency. In the past no satisfactory method has been available for direct separation of photosynthesis and respiratory activity in the light. The results obtained with more or less indirect procedures have been variously interpreted as indicating that under some conditions, at least, light may directly or indirectly stimulate respiration, may inhibit it, or may produce no effect at all upon it. Davis (39) found a more direct approach to the problem by utilizing for experimental study of the gas exchange, certain mutant strains of Chlorella that are green, that respire, and, when supplied with carbohydrate, can grow. They are, however, unable to carry out the photosynthetic process or evolve oxygen in the light. The rate of absorption of oxygen by cultures of these strains remained about the same throughout a series of 30-minute periods of light alternating with like periods of darkness, indicating that the light had no effect on the respiration of these strains. This result seems to be in line with the preponderance of evidence from other sources.

Most commentators on economic aspects of photosynthesis have emphasized the seemingly low average efficiency of the process rather than its truly gigantic proportions and the amazingly wide range in conditions under which it successfully operates. As regards photosynthetic efficiency in land plants, since the appearance of Brown and Escombe's classical paper in 1905 (25), it has been recognized that although absorption of the available carbon dioxide through the leaf stomata is highly efficient (24), in full sunlight the green leaf normally utilizes for actual photosynthetic activity less than 1 percent of the incident radiation. As to the magnitude of the process, only rough estimates have been possible because of the extremely diverse conditions of air, soil, and water over the earth's surface, which embraces about 35 billion acres of land and an area of 91 billion acres covered by the water. In view of the enormous carbon dioxide reserves of the ocean and the great depth to which its plant life extends, some authorities consider that its total photo synthetic output is many times that of the land (139). Apparently the average annual rate of carbon fixation on land is somewhat less than 1 ton per acre. Loomis (48) and other workers in this field consider that it may be of the order of 1,000 pounds. Applying even this low rate to the ocean as well as to the land, the yearly total of photosynthesis becomes 63 billion short tons of carbon.

PHOTOPERIODISM

Discovery

Demonstration of the phenomenon of photoperiodism by Garner and Allard in 1920 (60) brought into prominence for the first time the specific factor of *daily duration* as an element of the daylight complex capable of exercising qualitative control of the transition from the vegetative to the reproductive stage in angiosperms. The initial observations leading up to the discovery were made upon "Maryland Mammoth," a new horticultural variety of tobacco (*Nicotiana tabacum* L.) which appeared as a mutation in the very old Maryland Narrowleaf tobacco and upon certain medium and late varieties of soybeans. While the parent form of Maryland tobacco always flowered in midsummer or late summer at a height of about 3 to 5 feet, the Mammoth consistently maintained vigorous vegetative growth throughout the summer, attaining a height of 10 to 15 feet and unfolding more than 100 leaves. When propagated in the greenhouse in winter, however, the Mammoth form grew exactly like the parent form and readily flowered and matured seed.

In plantings of the soybeans made at intervals through the spring and early summer, all plantings of any particular variety tended to flower at about the same time in late summer or early fall, the vegetative periods progressively decreasing according to lateness of planting. Early varieties, on the other hand, remained vegetative for about the same number of days whether planted early or late. It became apparent that a definite seasonal effect was involved in the dependence of length of the vegetative period in certain varieties of tobacco and soybeans upon the date of planting. By means of extensive experimentation, differences in light intensity and temperature were excluded as possible causes of these seasonal effects.

To obtain direct evidence as to whether the seasonal change in length of the daylight period was involved, a very simple test was made. A small group of Maryland Mammoth tobacco plants growing in pots and a planting of Peking soybeans in a box, which had just begun flowering, were placed in a small, ventilated lightproof cabinet each day at 4 o'clock in the afternoon, beginning July 10 and were returned to direct sunlight each morning at 9 o'clock. In this way, the daily period of illumination of the test plants was reduced to 7 hours, whereas the midsummer period from sunrise to sunset at Washington, D. C., averages about 14½ hours. The experiment produced striking results--the tobacco plants were soon showing flower buds and promptly flowered and matured seed, while the soybeans matured their seed and shed their leaves a month earlier than control plants exposed to the natural daylight period. The tests with tobacco and soybeans were next extended to include fixed daily light periods ranging from 5 to 12 hours, always with corresponding control plantings exposed to the full natural daylight period of the open growing season. Numerous other plant species and varieties also were used. The Maryland Mammoth tobacco and the medium and late soybean varieties flowered with almost equal readiness in response to daily light periods of 5, 7, and 12 hours, although the height attained by the plants increased with increase in the light period. The vegetative periods of the medium, late, and very late varieties of soybeans under these light exposures were 21 to 28 days, while the controls remained vegetative for 51 to 62, 66 to 73, and 90 to 110 days, respectively.

Many other species, including Aster linariifolius, L., a tropical bean (Phaseolus vulgaris, L.), Cosmos bipinnatus Cav., and Bidens frondosa L., showed much the same response to the reduced daily light period as the Maryland Mammoth tobacco and the soybeans. Other species and varieties studied, however, responded differently to regulated daily light periods. In one group of these, such as spinach (Spinacea oleracea L), radish (Raphanus sativus L), and Hibiscus moscheutos L, reproductive activity was stimulated by the natural long summer daylight periods rather than by the shortened periods. A third group, including Connecticut Broadleaf tobacco (Nicotiana tabacum) and N. rustica, flowered with almost equal readiness under the full summer daylight period and the artificially shortened periods of illumination.

Further studies on plant response to the daily light period were made in the greenhouse during the winter. The natural short daily light period of winter was employed as the control and electric light of very low intensity switched on each day at 4:30 in the afternoon and turned off at midnight was used to extend the light period to 16 to 18 hours. The mean temperature of the greenhouse units was approximately 72° F. which is near the mean outdoor temperature at Washington during the summer. The results obtained were essentially the same as those applying to the open growing season. As a whole, the results showed that in some species and varieties flowering is stimulated by a short daily light period, in others the reproductive process is promoted by a relatively long daily period of light while still others are relatively indifferent to this factor. Midday darkening of the plants for 4 hours during the summer months proved to be far less effective than excluding early morning and late afternoon light in influencing time of flowering.

The term photoperiodism was coined to designate the effects of daily duration of light and the corresponding period of darkness. Photoperiodism was formally defined as "the response of an organism to relative length of day and night." With respect to the natural 24-hour cycle of day and night, this definition apparently is still applicable since it is rather generally considered that both the light period and the dark period are concerned in the photoperiodic response. For the sake of brevity, however, the expressions "length of day" and "day length" have been widely used in referring to the day-night relation. The term photoperiod, as now almost universally used, simply means the daily period of light in the natural 24-hour cycle or duration of the exposure to light in any other light-darkness cycle.

Garner and Allard (61) in their second paper published 3 years later showed that length of day, in addition to its effects on sexual reproduction, also strongly influences vegetative growth in various ways, including increase in stature, formation of bulbs and tubers, character and extent of branching, root growth, pubescence, pigment formation, seasonal leaf fall, dormancy, rejuvenescence, and death of the organism. Consideration was given also to interrelations of photoperiod and other factors of the environment. It should be noted that in these investigations very simple equipment was used throughout, in order to maintain at all times environmental conditions as closely comparable with those prevailing in nature as circumstances would permit. Various types of plant containers were used. Simple light-proof covers of cloth or other material were found satisfactory for regulating the photoperiod. For fairly large-scale operations, ventilated light-proof houses and small trucks mounted on steel tracks for conveying the plants into and out of the houses on fixed schedules were found to be quite convenient. During the summer season overhead electric lights were readily applied in the open to lengthen the light period. Artificial illumination for this purpose has been widely used in greenhouse work during the winter but certain limitations applying in this case, especially at high latitudes, are considered in a later paragraph (p. 32).

On the basis of the above findings, extensive research was soon undertaken in various localities dealing with numerous aspects of the photoperiodic reaction. Much of this research, especially in the earlier years, has related primarily to ecological and economic phases of photoperiodism. In general, the techniques employed also have been similar. It became apparent from the outset, however, that the clear-cut photoperiodic responses in floral initiation readily obtainable with many plants offered an attractive tool for searching study of the mechanism concerned in the transition from the vegetative to the reproductive state in seed plants. During the past two decades research in this field has been quite extensive and varied. This type of research, as well as study of interrelations of other environmental factors, has required development of many new techniques and improvements in equipment for obtaining and measuring precise data on the specific problems involved. During the progress of research in the two phases of the photoperiodic problem several reviews covering the whole field have appeared (20, 28, 58, 59, 69, 72, 73, 110, 118, 166) which supply a fairly comprehensive picture of the results obtained and the status in dealing with the major problems. Reviews of special features that have appeared are cited in later paragraphs.

Photoperiodic Classification of Angiosperms

Those plants that are distinctly sensitive to relative length of day and night can be readily arranged into two major groups: (1) flowering stimulated by relatively short days and (2) the flowering stimulus provided by relatively long days. Garner and Allard (61) classified the two groups as *short-day plants* and *long-day plants*, respectively (figs. 2, 3). Species and varieties showing only comparatively weak response to relative length of day and night with respect to flowering were allocated to a third class, *indeterminate* or *day-neutral plants* (fig. 4). This classification obviously rests on a purely factual basis and is independent of the mechanism or mechanisms concerned in the photoperiodic reaction.

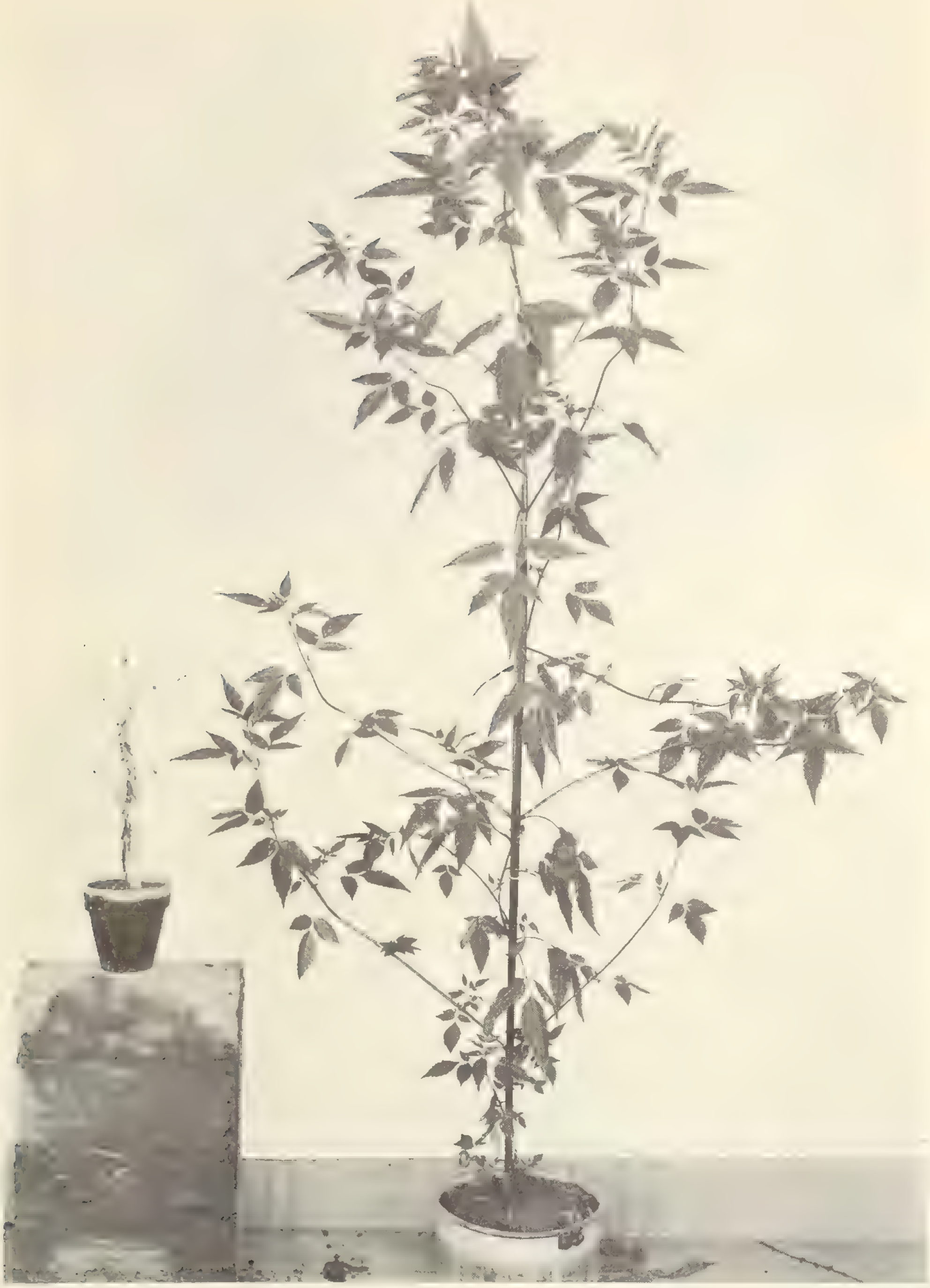

Figure 2.--A typical short-day plant, Bidens frondosa L. Plants from seed germinated December 1. Both were exposed to full daylight supplemented with low-intensity electric illumination from sunset to midnight for 60 days, after which the plant at left received only natural daylight. Shortening the photoperiod promptly stimulated flowering and when photographed April 17, the plant had matured seed and was dead, at a height of 15 inches. Plant at right, exposed to the lengthened photoperiod throughout, had reached a height of 6 feet and remained strongly vegetative. (From Jour. Agr. Res. 27: 119-156. 1924. W. W. Garner, C. W. Bacon, and H. A. Allard.)

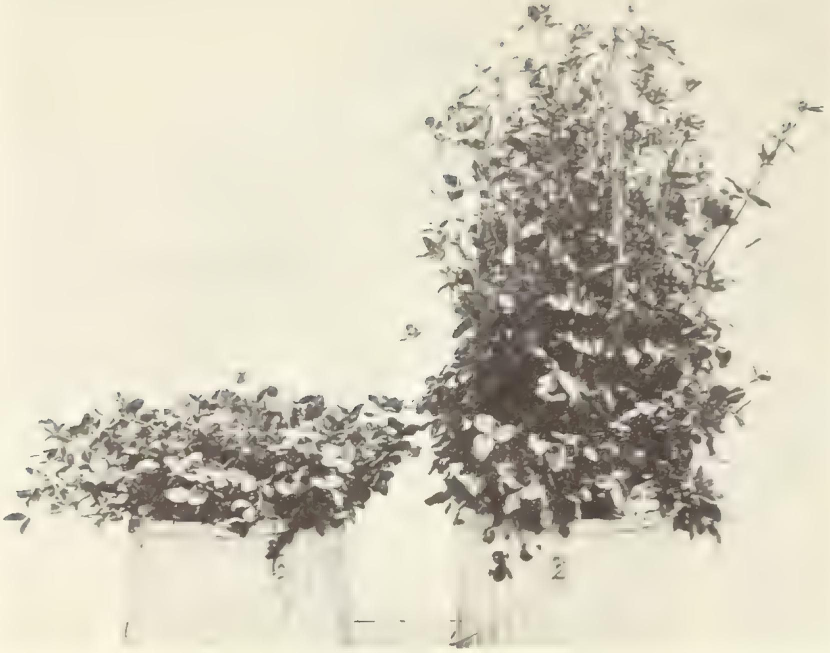

Figure 3.--A well-defined long-day plant, red clover (*Trifolium pratense* L). Plants at left were exposed to a 10-hour day while those at right received the full natural length of day through the spring and early summer. Red clover remains purely vegetative, with a prostrate type of growth, for an indefinite period when exposed to a 10-hour photoperiod. (From USDA Yearbook Sep. 852: 377-400, 1920.)

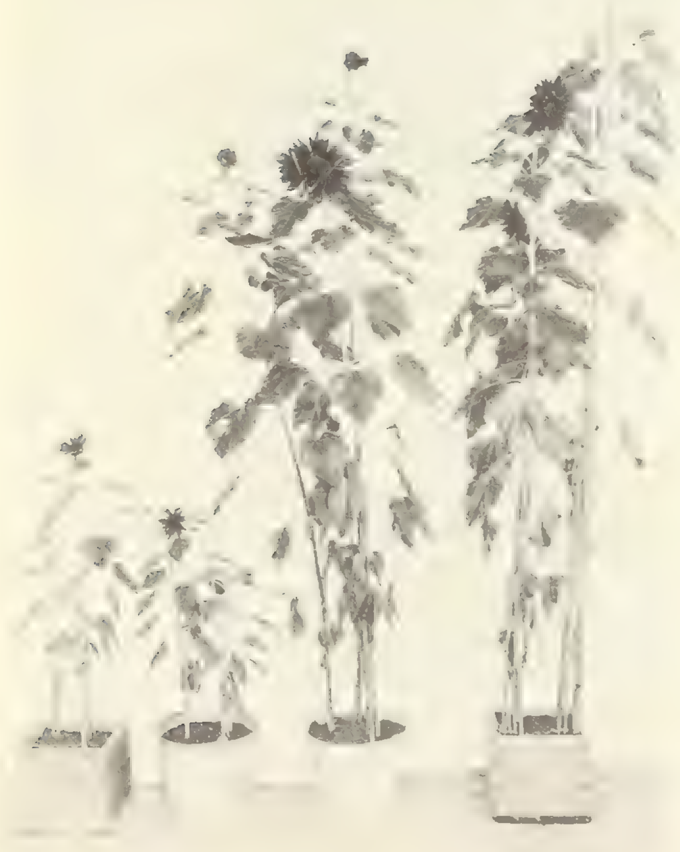

Figure 4.--*Helianthus annuus*, L., a day-neutral plant. Beginning with germination, January 23, the large plants at right were exposed to the full day of late winter and spring, while the smaller plants at left received only 7 hours of light daily. Photographed May 14. Despite the strong contrast in rate of growth, there was no difference in time of first flowering under the relatively long and short photoperiods. When the photoperiod was increased to 18 hours there was a slight delay in the date of flowering. Obviously in this species the effects of photoperiod are essentially of a quantitative rather than a qualitative nature. (From Jour. Agr. Res. 27: 119-156. 1924. W. W. Garner, C. W. Bacon, and H. A. Allard.)

The *maximum day length* in which flowering ordinarily takes place in short-day plants and the *minimum day length* required for flowering in the long-day group were called the *critical lengths of day*. The distinction thus drawn between the short-day and long-day groups, as such, is important. In both groups the actual critical day length varies with the species, variety or strain; but for most members of the short-day group this falls within the range of 13 to 16 hours and in the long-day group the usual range falls within 14 to 10 hours. Short-day plants tend to remain vegetative for long periods in all day lengths in excess of the critical and long-day plants tend to continue vegetative activity in day lengths shorter than the critical. Thus, the significance of the critical length of day does not rest simply on its absolute length but also on the contrasted types of response to light periods below and above it (*57*).

Comparison of the complete photoperiodic reaction curves for the more typical short-day and long-day plants is helpful in bringing out the contrast in response of the two plant types to the light period. The essential characteristics of the typical photoperiodic action curves for the two plant types are shown in figure 5. Apparently, very few complete reaction curves of this sort have been worked out but an excellent example is afforded by Lang and Melcher's (*95*) detailed study of the photoperiodic reaction in *Hyocyamus niger*, which is representative of the long-day type. In figure 6, taken from an article by Steinberg and Garner (*155*), which deals primarily with the interrelations of photoperiod and temperature, photoperiodic curves that are almost complete, are shown for the short-day types, Mandarin, Peking, and Biloxi soybean at four different temperature levels.

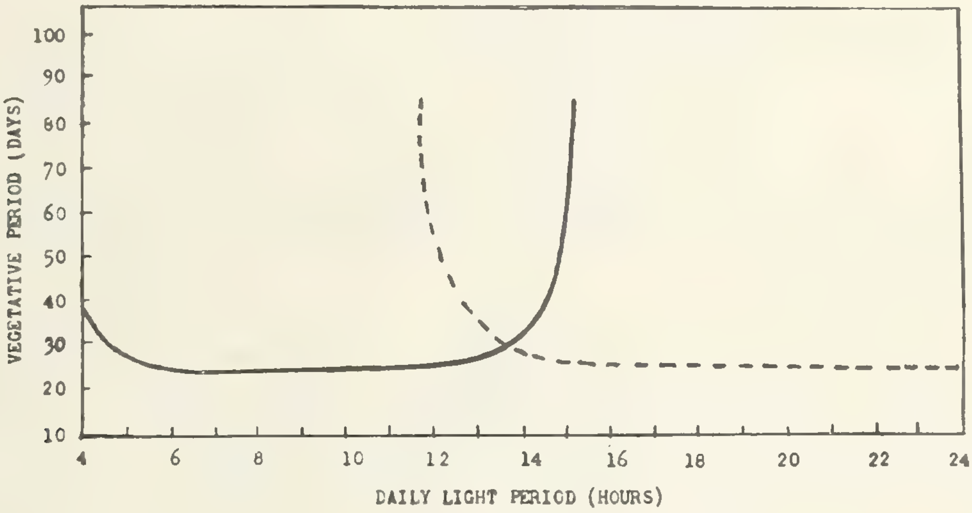

Figure 5.--General form of the complete photoperiodic reaction curves applying to the greater portion of the sharply defined short-day and long-day plants. The form of curve shown at left, representing the more typical short-day plant group, includes a definite *upper* critical photoperiod together with the approach to it from a relatively wide band of shorter optimal and near-optimal photoperiods, but in many cases it lacks a clear-cut lower critical light period. The form of curve at right exhibited by typical long-day plants differs essentially from the short-day plant curve in that it includes a well defined *lower* critical light period while an upper critical photoperiod is entirely lacking. (Previously unpublished.)

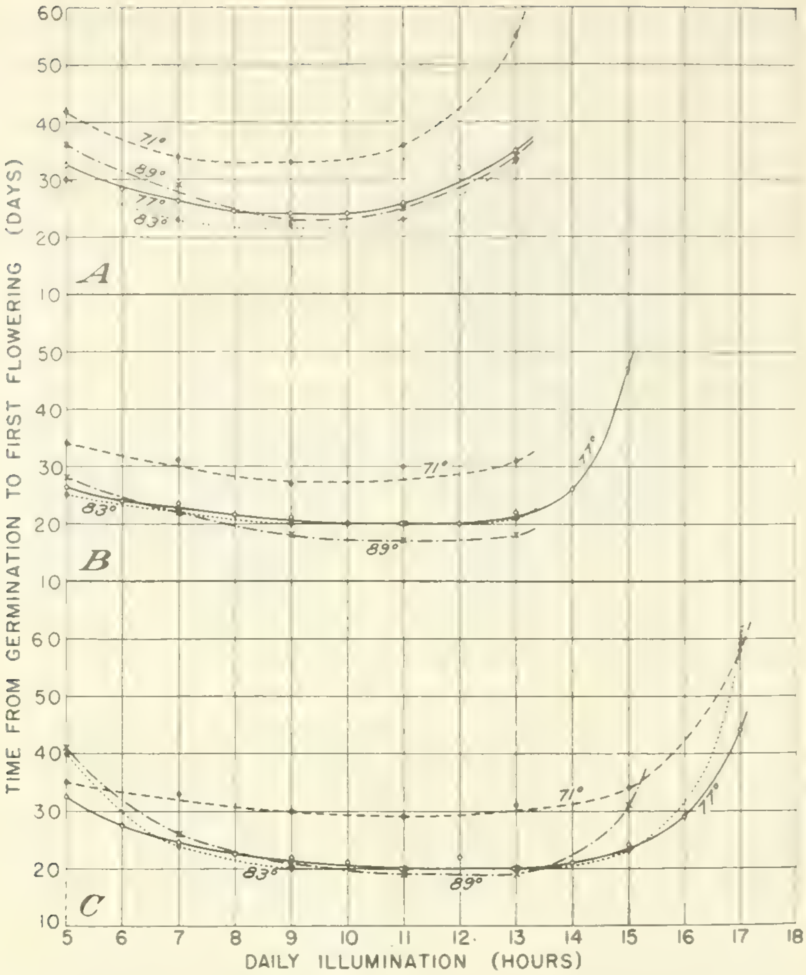

Figure 6.--Effect of photoperiod on time of first flowering in the Biloxi (A), Peking (B), and Mandarin (C) varieties of soybean grown at fixed temperatures of 71°, 77°, 83°, and 89° F. In the tests at 77° the interval between successive photoperiods was 1 hour and at other temperatures it was 2 hours. In each variety, flowering was considerably delayed by the lowest temperature, 71°, under all photoperiods. The other temperatures produced comparatively little effect as result of photoperiod. (See Literature Cited 155.)

Short-day plants differ among themselves as to the range in day lengths below the critical in which they readily flower. Peking soybeans, with an upper critical day length of approximately 15 hours, flowered with almost equal readiness under all photoperiods ranging from 4 to 13 hours when grown in a favorable environment but were unable to survive under a 3-hour photoperiod, apparently because of unfavorable nutrition conditions (155). Similar results have been reported with hemp (104), late-maturing rice (90), and other short-day species or varieties (100). With photoperiods of less than 4 or 5 hours, growth and even survival of the plant become chiefly dependent upon photosynthesis, with quantity of illumination the limiting factor. Under these conditions intensity and daily duration of light become strongly compensatory. It appears, therefore, that under normal conditions some short-day plants can hardly be considered as having a typical lower critical day length. On the other hand, Tephrosia candida grown in the open under subtropical conditions was found to flower readily when exposed to a 12-hour day but remained vegetative under a 10-hour day and under the maximum natural day length of 13.2 hours (102). Obviously this species has a well-defined lower critical photoperiod.

Several other species also have been reported as showing very narrow flowering responses to day length (4). A great many occupy positions between these two extreme classes with respect to range in photoperiods favorable to flowering. Since the critical light period necessarily corresponds to a nicely balanced condition in the plant between vegetative and flowering tendencies, it is to be expected that in this situation other disturbing factors of environment will exert their maximum effects in modifying the response to photoperiod, including possibly, limited shifting of the critical photoperiod itself (95). The day-neutral plants show quantitative responses to photoperiod, such as extent or amount of flowering and fruiting but have no critical day length, since they flower more or less readily in either short days or long days (fig. 4). Assignment to this class is somewhat arbitrary since plant species and varieties exhibit all degrees of acceleration or delay in flowering in response to photoperiod.

For purposes of orientation with respect to the long-day and short-day types, it is to be noted that responses to photoperiods covering the range of 10 to 16 hours are not adequate in themselves but if supplemented with data for photoperiods of 9 and 18 hours ordinarily should yield decisive results. This situation is well illustrated by the behavior of the Mandarin soybean. As shown in figure 1, this variety, when grown under conditions that are otherwise favorable, exhibits a relatively fixed vegetative period of about 20 to 24 days throughout the year at Washington, D. C., with the effective length of day ranging from approximately 9.5 to 15.5 hours. On this basis, the typical photoperiodic response of the day-neutral type is shown. However, as is shown in figure 6, when the range in photoperiod is extended to include a 17-hour day, the Mandarin definitely behaves as a short-day type, even though it has an exceptionally long critical photoperiod.

Much of the literature on photoperiodism is based on this system of classification and much of it is concerned with the contrasted photoperiodic responses of the long-day and the short-day plant types under a great variety of conditions. Many commentators, however, have regarded this classification as inadequate in view of later developments, mainly on grounds that:
(1) Temperature or other factors may modify photoperiodic responses;
(2) plant species as such cannot be satisfactorily classified under the scheme; and (3) the various phases of sexual reproduction differ somewhat in their photoperiodic requirements. Each of these matters is briefly considered in subsequent sections. It will suffice to point out here that the classification as originally proposed was based essentially on contrasted flowering responses (anthesis), these contrasts primarily relating alone to varieties and strains within the species and when these were grown under conditions to which they are adapted. Under these limitations, the classification still appears to be valid, as far as it goes.

Adaptation and Distribution

Sharp seasonal contrasts in growth and development observed in certain horticultural varieties of tobacco and soybeans are linked with the natural seasonal changes in relative length of day and night at once suggested that latitudinal differences in day length would be found to have important bearing on plant adaptation. Comparable day length responses of species and of varieties derived from various latitudes served to strengthen this hypothesis. Following these results, many workers undertook research on various aspects of plant adaptation and distribution as influenced by combined latitudinal and seasonal changes in length of day. The research in this field has extended from the equator to well within the Arctic Circle (1). A large volume of literature has accumulated on the subject. Specific features of special interest are briefly considered in later paragraphs.

After an elaborate study of "photoperiodic adaptation" in species from the tropics, the temperate zone, and the Arctic region, Lubimenko and Szeglova (100) concluded that the reaction to length of day is conditioned by the geographical latitude of the native habitat. They found that Arctic plants require long days or continuous illumination, tropical plants require short days, but temperate zone plants require intermediate days and may be of either the long day or short day type. In comparative studies of cereals, flax, beans, and peas in relation to the geographical latitude of their origin, Doroshenko and Rasumov (42) found that for the most part the southern forms reacted more favorably to artificially shortened day lengths than the northern forms--in Leningrad. In comparing regulated photoperiods of certain Australian, English, and Welsh varieties of wheat, Forster and associates (46) found that varieties originating in Australia--where the days are shorter--in all cases developed spikes under shorter light periods than the English and Welsh varieties which usually grow under a much longer summer-day length.

There is some evidence to indicate that, at least in part, plants tend to become increasingly sensitive to photoperiod with decrease in latitude. In Puerto Rico with a maximum change in length of day through the year of only 2.2 hours, McClelland (102, 103) has reported some striking photoperiodic responses in both wild and economic species. Most observations on photoperiodism in the tropics have dealt with economic species and varieties (149), although it has been reported that with a comparatively uniform climate in other particulars near the equator, slight seasonal changes in length of day apparently induce definite periodicity in flowering in many wild species.

In Solidago sempervirens L., which occurs along the Atlantic Coast from Newfoundland to Mexico, the mean date of flowering in the fall becomes progressively later with decrease in latitude (67, 68). Collections of this species from northern and southern areas maintained the differences in date of flowering when all were grown at Rochester, N.Y., indicating a genetic basis for these differences, but both the early and the late forms responded to shortened photoperiods.

Similarly, side-oats grama grass, Bouteloua curtipendula (Mich.) Torr., is found from Saskatchewan across the United States and southward into Mexico (122). Olmsted (122) found that when strains of this species were grown under various regulated photoperiods in greenhouses, those from southern Texas and Arizona consisted almost entirely of short-day or intermediate plants with an upper critical day length of 14 to 16 hours. A North Dakota strain consisted largely of plants exhibiting long-day characteristics with a critical photoperiod of about 14 hours. Strains from intervening areas also contained many plants with long-day tendencies but showed somewhat greater diversity in response with decreasing latitude. In flowering and other responses, the various geographic strains were found to be well adapted to the range of photoperiods during the growing seasons of their native environments.

Strong evidence shows that in woody plants photoperiodic response is an important factor in their growth period and in their adaptation to different latitudes. Species of southern origin commonly show very late growth when propagated in high latitudes; but, if subjected to shortened photoperiods, vegetative activity ceases much earlier. There are, likewise, early- and late-flowering forms of woody species corresponding to seasonal change in length of day in low and moderately high latitudes.

The evidence as a whole clearly indicates that photoperiodic reaction in species, varieties, and strains is conditioned largely by the latitude of origin. Southern forms exhibit chiefly the characteristics of the short-day type, those of intermediate latitudes consisting alike of long-day, day-neutral, and short-day plants, while the northern forms are composed mostly of typical long-day plants. In moderately high latitudes many short-day plants are more successful or more productive than near the equator, because they are able to make extensive growth during the long days of early summer and to flower and produce seed abundantly during the decreasing photoperiod of late summer. At very low latitudes short-day plants are forced into flowering and fruiting before they are able to make much growth, and yields of total dry matter and of seed are necessarily poor.

A considerable number of investigators have undertaken to assign various species to the long-day or short-day groups on the bais of the photoperiodic reaction of only one or at most, a very few of their constituent varieties or strains. Conclusive evidence, however, shows that most species contain varieties or strains with clearly defined contrasts in their photoperiodic reaction. This is especially true of species having a wide latitudinal distribution (122). On the other hand, these photoperiodic differences of varieties and strains within the species normally relate only to variations in length of the critical photoperiod and differences in sensitivity to the length-of-day factor. In other words, a given species is usually composed only of long-day and day-neutral or short-day and day-neutral forms. The more typical short-day and long-day types are rarely found in the same species.

As illustrative of the intimate bearing of photoperiod on seasonal adaptation of species and varieties at a given latitude, the photoperiodic reaction of the Peking and Biloxi soybean varieties grown at various seasons of the year at Washington, D. C., under favorable temperature conditions is of considerable interest (63). As shown graphically in figure 1, the late variety, Biloxi, shows the characteristics of an early variety if germination takes place within the period, September 1 to March 15, during which the length of day does not exceed 13 hours. Plantings germinating in late March abruptly change over from spring flowering to fall flowering as the day length comes to exceed the critical. These later plantings, of course, make much larger growth than the earlier ones. In this changeover the vegetative period increases from about 26 to a maximum of 145 days. The medium variety, Peking, shows the same type of photoperiodic response as the Biloxi, but the changeover from spring flowering to late-summer flowering is less abrupt and takes place 6 weeks later. The crop yield of Peking may be smaller than that of Biloxi, but escape from frost injury is more certain.

Sexual Reproduction

The photoperiod may affect growth and differentiation in all parts of the plant and the associated physiological processes as well, yet from the beginning interest has been centered chiefly on the formation and development of flowers, fruits, and seeds. Observations on the reproductive phases in most of the early work were based chiefly on the unfolding of the flowers (anthesis) and maturation of fruits and seeds. This was done because at that stage investigators quite naturally were concerned primarily with ecological and agronomic aspects of photoperiodism, for obviously adaptation, distribution, and survival depend on successful production of fruits and viable seeds rather than mere initiation of flower formation. From this point of view, photoperiodic classification, likewise, logically would rest on the same basis. On the other hand, in dealing with photoperiodic response from the standpoint of the physiology of flowering, floral initiation--the transition from the vegetative to the reproductive state--becomes a major consideration, although all phases of the reproduction process are of interest.

Photoperiod may influence more or less independently the various phases of the reproductive process, from floral initiation to seed maturity. In some species there are material differences between the optimal photoperiods for some of these phases. For example, Ball (12) found that in numerous species growing in Ceylon, overnight illumination inhibited anthesis in flowers that already had developed to the state where normally they would have opened on the following day. In several species growing in the long days of the British Isles, however, the nocturnal illumination was wholly ineffective in preventing anthesis. These contrasting results, of course, are in line with the normal over-all responses of short-day and long-day plants, but they clearly show that floral initiation, in itself, may mean little with respect to successful flowering and fruiting in response to photoperiod. Again, development and ripening of seeds in Peking soybeans are greatly accelerated by exposure to a short photoperiod after flowering has already taken place (60). In winter cereals floral initiation takes place under short days in association with low temperature while earing is accelerated by long days. Similar differences on optimal photoperiods for flowering and for fruiting have been observed in a considerable number of species. This is not surprising since, as a rule, the length of day is constantly changing as the plant passes through the successive stages of the reproductive process. In many cases, however, these differences in photoperiodic requirements involve only quantitative rather than qualitative effects on the several stages of the reproductive process, such as limited acceleration or delay in development of flower or fruit or changes in yield of these.

Although there may be exceptions, in short-day plants maximum acceleration of flowering usually occurs under photoperiods well below the critical, but maximum fruitfulness is favored by light periods considerably nearer the critical since the size attained by the plant usually is proportional to the length of the photoperiod. In long-day plants, earliest flowering as well as maximal fruiting, as a rule, are favored by photoperiods far above the criticals, oftentimes even by continuous light. In the immediate vicinity of the critical photoperiod there is a condition of balance between vegetative and reproductive activity and, consequently, there is a tendency toward the ever-blooming condition, that is, prolonged growth accompanied by continued but sparse flowering. Naturally, this tendency is most pronounced in plants that do not exhibit a sharply defined critical photoperiod.

Several investigators have shown that changing photoperiod may profoundly affect development of the sex organs (98). Very short light periods have been found to cause abnormalities as formation of pollen in ovules and embryo sac differentiation in anthers. Schaffner (145) and several other investigators obtained, in certain forms of *Zea mays* exposed to the short but gradually changing day length of winter, varying degrees of female expression in the terminal tassel, including appearance of silks and seeds. In greenhouse plantings of *Cannabis sativa* L. made at intervals through the decreasing length of day of fall and early winter, there was a constantly increasing percentage of sex reversal among staminate plants (146).

Growth Effects

The effects of photoperiod on the many features of plant growth are extremely varied and oftentimes very striking. According to Harder and Witsch (79), exposures to long day and short day, respectively, produce such contrasts in the appearance of the short-day plant, *Kalanchoe blossfeldiana*, that only with difficulty can it be recognized as the same species under the two conditions.

In the short-day type, the rate of plant growth as a whole usually is directly proportional to length of the photoperiod up to the critical for flowering. Floral initiation checks growth but exposure to photoperiods above the critical in most cases leads to further increase in growth rate and accumulation of dry matter. In some short-day plants, however, best growth takes place under intermediate day lengths.

Probably most long-day plants increase their growth rate with increasing length of day up to 16 to 18 hours. Apparently most if not all Arctic species make their greatest growth in continuous light (1, 100). With several species adapted to high latitudes, Smith (152), however, found that while in the early stages maximum growth took place under continuous light but as the plants increased in age maximum growth rate shifted toward the shorter photoperiods. A considerable number of temperate zone species have shown more or less injury and reduced yield of dry matter when grown in continuous light consisting in part of supplementary artificial light. It appears that these effects have been due, at least in part, to excess infrared radiation or other abnormalities in the artificial light sources employed (83, 180). It is not clear as to whether all of these species could tolerate continuous sunlight under temperate zone conditions (7).

Each organ of the plant may have an optimal photoperiod for growth which may materially restrict growth of other organs (100). In most, though not all species, stem elongation or increase in stature is accelerated by increasing photoperiod up to 16 hours or longer (163). The accelerated rate of stem elongation under long-day conditions is associated with both an increase in number of nodes formed and in length of internodes (fig. 6). Short-day annuals may attain heights far above normal when exposed to a long photoperiod for prolonged terms.

In many long-day plants there is little or no elongation of the axis with photoperiods below the critical, even over long periods of time. In some instances transfer of this type from long-day to short-day conditions after stem elongation has commenced, may inhibit flowering and the growing point will develop a rosette. When the photoperiod becomes suboptimal for elongation of the stem, one of the typical effects of the resultant partial loss of apical dominance is promotion of branching which may or may not be associated with flowering. In the flowering stem, branching commonly occurs in the upper part but with further shortening of the photoperiod the branching tends to become basal, somewhat as in the tillering of cereals. Finally, a relatively short photoperiod may induce elongation of underground stems (61, p. 876).

Maximum relative production of leaves has been found in most instances to take place under short photoperiods. As stem elongation decreases, the proportion of leaves increases, and in many long-day plants photoperiods shorter than the critical stimulate extensive and continuing leaf development for indefinite periods of time--oftentimes with no elongation of the axis. The increase in stature that usually takes place in both long-day and short-day plants, when exposed to photoperiods above the critical, results in an increase in absolute number of leaves and in larger leaves.

In many plant species, including representatives of the long-day, short-day, and day-neutral types, growth of root and of shoot are affected to approximately the same degree by change in the length of day (172). This suggests a rather close correlation between the absorbing and transpiring systems. Accordingly, root growth tends to decrease with decrease in photoperiod. In numerous species, however, the root undergoes more or less thickening under the influence of a short photoperiod.

Tubers, Bulbs, and Thickened Roots

Formation of tubers and other comparable storage organs constitutes a prominent feature of photoperiodic response (61). Numerous observations have shown that development of tubers, bulbs, and thickened roots is promoted by photoperiods which inhibit or check vegetative growth, especially the elongation of the axis. This relationship applies to tuberization of aerial axillary buds in such species as *Dioscorea divaricata* L. as well as to underground structures. Photoperiods that are unfavorable to elongation of the stem also may induce thickening of nodes in nontuber forming plants, such as soybean. In annuals and biennials that do not develop an axis under reduced photoperiods, such as radish and beets, the root may continue to thicken for prolonged periods as a result of the continued activity of the leaves. Since maximum growth is attained by most plants under the influence of long photoperiods, it is not surprising to find that in the great majority of tuber-forming species tuberization is most intense under decreasing light periods. Tuberization as a feature of photoperiodic response is of considerable interest, because it furnishes direct proof that the inhibition of vegetative growth by decreasing day length is not due to failure of the carbohydrate supply--at least in the tuber-forming species.

Because of the great economic importance of the Irish potato, its response to photoperiod, along with temperature and light-intensity interrelations, has been extensively investigated in Russia, Germany, Great Britain, and America, mainly with respect to seasonal and latitudinal adaptation of northern and southern species and varieties, both wild and cultivated. The literature has been reviewed by Driver and Hawkes (43).

In most tuber-forming plants, including various species of Solanum, vegetative increase is stimulated by a long photoperiod, while flowering and seed formation as a rule are more or less depressed by decreasing day length. With decreasing photoperiod the ration of leaf to stem increases. Varieties of *Solanum tuberosum* differ sharply in their response to photoperiod, with respect to tuber formation. Some varieties adapted to high latitudes readily form tubers in response to long photoperiod and relatively low temperature. These varieties commonly produce the early crop. Varieties producing the late crop in temperate regions, however, form tubers freely only under a decreasing length of day.

Most intensive tuberization takes place under a short photoperiod. Maximum production of tubers usually occurs under short photoperiod after extensive growth has been stimulated by longer photoperiod. Since most potato species and varieties do not show qualitative responses to photoperiod, with respect to flowering, some investigators have classified them into short-day, long-day and day-neutral on the basis of tuber formation. This method of classification, however, tends to cause confusion.

The photoperiodic response of onion, *Allium cepa* L., differs markedly from that of the tuber-forming species. In general terms, in photoperiods less than 10 hours, the vegetative stages continue more or less indefinitely, whereas photoperiods more than 12 hours stimulate flowering and formation of normal bulbs (*61*). There are pronounced varietal differences in optimal light periods for formation of bulbs, which largely explain their differences in latitudinal adaptation (*103*, *105*). Forms adapted to the Far South produce bulbs in day lengths of 10 to 12 hours but the Northern States storage varieties require photoperiods up to 15 or 16 hours for bulb formation. Increasing day length hastens maturity in all varieties.

Woody Plant Responses

Woody plants show the same contrasts as herbaceous species with respect to photoperiodic requirements for flowering. Thus, the three shrubs --*Hibiscus syriacus* L., *Malvaviscus conzatti* Greenmann, and *Buginvillea glabra* Choisy--have been found to respond as typical long-day, day-neutral, and short-day types, respectively (*3*). Leaf fall in deciduous species is strongly influenced by photoperiod. Specimens such as *Rhus glabra* L., *R. capallina* L., and *Liriodendron tulipifera* L., when exposed to a 10-hour photoperiod through the summer season, retained their leaves but made little or no upward growth (*54*). The leaves developed a dark-green color and appeared to contain but little sap. When other specimens growing under full day were transferred to a warm greenhouse in September, all soon shed their leaves and became dormant under the decreasing length of day. When weak supplemental electric light was used to provide a 16-hour photoperiod for a parallel series, *Rhus capallina* shed its leaves only after considerable delay, *R. glabra* retained its leaves all winter, and *Liriodendron* retained its leaves and continued active growth throughout the test. These results suggest that gradual decrease in day length rather than abrupt change from long to short photoperiod favors leaf fall.

From experiments conducted in the region of Leningrad, Moshkov (*113*) concluded that differences in degree of frost resistance of a given species in different latitudes is determined by photoperiodic conditions during vegetative growth period. In some species adequate resistance to frost was developed by exposure to a favorable photoperiod for only 20 days.

Kramer (*92*) found that in all broadleaved and coniferous species growth ceased as early in the fall in a warm greenhouse as in the open. A long photoperiod accelerated resumption of growth after dormancy in numerous species. In tests with coniferous and broadleaved species exposed to natural day, with and without supplemental illumination, in the greenhouse and outside, Jester and Kramer (*82*) observed that northern species made greater gains in height under continuous light than when exposed to a long photoperiod, and failed when exposed to the short natural day. In the greenhouse many species grew all winter under continuous light. The deciduous species held their leaves longest when exposed to long day and continuous light. Several reports have appeared showing the effects of street lights in delaying leaf fall in nearby trees. In some instances considerable frost injury has been observed to occur where the lights have stimulated continued vegetative activity beyond the normal time for cessation of growth.

Photoperiodic After-effect

To bring about flower formation in either long-day or short-day plants, it is only necessary that the favorable photoperiod act for a certain minimum length of time regardless of the photoperiodic conditions to which the plants are exposed subsequently (61, 141). The changes in the plant, which are brought about by the light period, during the limited time required and resultant flowering, are known as "photoperiodic induction." Species, varieties, and strains differ widely on their photoperiodic induction.

In the short-day plant, Biloxi soybeans, only 2 or 3 short days (and long nights) are required for stimulating development of flower primordia, although 8 or 10 short photoperiods are needed for free flowering (18, 61). In other species or varieties much longer exposure to the proper photoperiod may be required for completion of photoperiodic induction.

Young plants do not become sensitive to photoperiod with respect to floral initiation until they have fully expanded one or more foliage leaves. It appears that in some cases flowering occurs in older plants when they are exposed to photoperiods under which they remain vegetative during their earlier growth. This situation does not apply generally, however. For example, Sedum spectabile maintained under a 12-hour day during the summer and the natural day length and temperature of winter over a continuous period of 9 years at Washington, D. C., remained vigorous but strictly vegetative throughout and then flowered at the same time as the controls, when exposed to the natural summer length of day (65). Similarly, Hibiscus syriacus L. remained vegetative for 4 years under a 10-hour day at Washington; red clover subjected to a 10-hour day failed to flower over a 4-year period in Wales (164); late rice under continuous light continued vigorous vegetative activity for 3 years and then flowered normally and matured seeds when exposed to a short day, in Japan (90).

It is considered that a true photoperiodic aftereffect applies only to acceleration of reproductive processes and development of the organism and not to stimulation of vegetative activity. Hence, only short-day plants may be expected to show a short-day aftereffect and only long-day plants would show a long-day aftereffect. The above-mentioned results obtained with Sedum, Hibiscus, red clover, and late rice seem to be in accord with this concept.

The photoperiodic carryover effect in floral stimulation may persist for long but varying periods after the treated plants are subjected to photoperiods favoring vegetative activity. Evidence of a tendency toward renewal of vegetative increase soon appears. In some cases there is a relatively rapid return to full vegetative activity. In any event, the end results in annuals and herbaceous perennials are quite different than those applying to these plant types when exposed continuously to photoperiods favoring sexual reproduction. In the latter case annuals, of course, usually decline rapidly and die after flowering and fruiting and the perennials soon pass into a state of dormancy. Under the influence of photoperiods favoring vegetative activity, on the other hand, the previously acquired flowering stimulus constantly tends to grow weaker and oftentimes instead of death or dormancy, rejuvenation is effected. Rejuvenation may take place even when the shift to photoperiods favoring vegetative activity does not occur until after the plants have flowered (60).

The photoperiodic aftereffect obviously is of interest to ecologists for the reason that over most of the earth's surface the length of day is constantly changing. This carryover effect has been widely employed in investigations relating to the physiology of flowering since it provides a convenient means of obtaining quantitative data on various phases of the photoperiodic reaction under controlled conditions. For example, to study the effect of light intensity on photoperiodic induction, cultures of a typical short-day plant may be grown for a time under a long photoperiod, after which parallel groups are given, say, 2, 4, 6, 8, and 10 exposures, respectively, to short photoperiod at two or more intensity levels. After the treatments, all groups are returned for a definite time to the long photoperiod and then examined quantitatively for presence of flower primordia, and for other observations of interest.

Abnormal Photoperiods and Cycles

In early photoperiodism studies it was observed that midday darkening of plants for several hours is not effective in inducing flowering in the short-day type or in inhibiting it in the long-day class of plants. Subsequently, extensive studies were conducted in the growing of plants with various cycles of light and darkness other than the daily cycle of 24 hours prevailing in nature and with many different combinations of the periods of light and darkness composing the cycles.

The primary object of the tests was to obtain further information on the relative significance of the light period and the dark period in photoperiodic induction. Results obtained with daylight are more directly comparable with the characteristic responses applying to the natural 24-hour cycle, but, unfortunately, the possibilities in this direction are limited. Darkening the plants from 10 a.m. to noon and from 2 to 4 p.m. each day reduced growth but had no significant influence in initiating sexual reproduction in short-day plants or in inhibiting it in long-day plants. Exposing a group of short-day plants alternately to a 10-hour day and the full summer day length of about 15 hours gave results falling between those of a short day and a long day, with respect to flowering. On garden balsam, a long-day type, there was no formative effect. When the plants were completely darkened on alternate days, whereby they received 15 hours of light in each 48-hour cycle, a weakened short day effect was produced on both short-day and long-day plant types (64).

In a study of the effects of relatively short photoperiods and dark periods of equal duration, Garner and Allard (64) grew a considerable number of species and varieties representing both the short-day and long-day types in electric light of high intensity. In one series the alternating light and dark periods ranged from 1 hour down to 5 seconds, with intervening periods of 30, 15, 5, 1, 1/4 minutes, each series receiving a total of 12 hours of illumination per day. The results were surprising. In all cases the effect on floral initiation was essentially that of a long day or continuous light. In other words, flowering was stimulated in the long-day plants and inhibited in the short-day group.

On the other hand, there were striking differential effects on growth and general nutrition of the plants that applied alike to the short-day and long-day types. The contrasting effects included sharp differences in stature, chlorosis, and necrosis in foliage leaves and attenuation. The injurious effects increased with decrease in duration of the light-dark alternations down to about 1 minute, whereas further shortening of the intervals brought improvement and the 5-second alternations gave approximately normal growth and development. Among the species and varieties of plants used in these tests were Biloxi and Peking soybeans, _Perilla frutescens_, _Cosmos bipinnatus_, _Tithonia tubaeformis_, _Rudbeckia bicolor_, _Delphinium ajacis_, and _Steironema ciliatum_.

In later tests, Allard and Garner (5) grew some of these and certain other varieties and species in longer alternations of light and darkness ranging from 7 to 36 hours, under accurately controlled conditions of temperature and humidity. Except for alternations of light and darkness not far removed from 12 hours, there was in all cases a tendency to inhibit flowering in short-day plants and to induce it in long-day plants. Combining the results of the two series of experiments, it appears that in Peking soybean, a short-day type, with a critical day length somewhat longer than that of the Biloxi variety, alternations of light and darkness ranging from 5 seconds up to and including 8 hours in duration tend to inhibit flowering, as do also alternations of 16 hours or longer, while intermediate intervals of 9 to 14 hours' duration induce flowering.

The long-day type, _Rudbeckia_, tends to respond in just the reverse manner to the various cycles of light and darkness. Hamner (71) and several other workers have conducted somewhat similar experiments with Biloxi soybean and cocklebur, employing a wide range of photoperiods, combined with a fixed dark period, many dark periods, and a fixed photoperiod and still other alternations of light and darkness. The results as a whole seem to demonstrate that photoperiodic induction in short-day plants is a result of the combined action of a photoperiod of the proper duration and a dark period of the necessary length.

It has been ascertained that photoperiodic induction does not take place in short-day plants if the necessary dark period is broken into two short periods by even a brief interval of light (74). It has been shown, also, that the same procedure overcomes the inhibiting action of a long dark period on flowering in long-day plants.

Light Intensity and Quantity and the Photoperiodic Reaction

The phenomenon of photoperiodism rests essentially on the principle that within rather wide limits light of relatively low-intensity acting for a relatively long period does not influence plant growth and development in the same manner as does light of high intensity acting for a reduced period of time. Of course, normal photoperiodic response will be possible only so long as the light energy meets the minimum requirements for photosynthesis and other basic nutritional needs of the plant. It is generally recognized that for the majority of plants growing in open situations the maximum intensity of daylight is much higher than is required for favorable growth and development.

As a part of the early work on photoperiodism it was shown experimentally that reduction of the summer daylight intensity to one-third by shading had no significant effect on the sharply defined photoperiodic response of several soybean varieties (61). In another experiment, reduction of 2.5 percent in the quantity of sunlight received daily, when brought about by excluding the early morning light was far more effective in accelerating flowering in Peking soybean than a reduction of 65 percent accomplished by darkening the plants from 10 a.m. to 4 p.m. The fact that very weak artificial light, when used to extend the natural daylight period, is effective in producing the characteristic long-day photoperiodic effect further indicates that within a rather wide range quantity of illumination in itself ordinarily is not a decisive factor in the photoperiodic reaction.

In many plants fairly high illumination intensities are required for normal functioning of photosynthesis and other physiological processes bearing on photoperiodic response. Harder and associates (77) concluded that for long-day plants 20 percent of the normal daylight intensity of the growing season is fully effective in photoperiodic induction. Considerable evidence indicates that intensities of approximately 1,000 to 2,000 foot-candles may be required to insure clear-cut response in plants generally.

It is well known that in most sun plants photosynthesis tends to increase with increase in light intensity up to 20 percent or more of full daylight. In this connection, Parker and Borthwick (128) found that under certain conditions a favorable inductive cycle failed to bring about floral initiation in Biloxi soybean when the plants were deprived of carbon dioxide. Hamner (71) showed that for maximum effectiveness in initiation of floral primordia in Biloxi soybean, when subjected to appropriate photoperiods, a minimum light intensity of 800 foot-candles is required. Even under continuous illumination, intensities of more than 700 foot-candles are required for flowering in annual beet (120). It seems likely, therefore, that low daylight intensity may become an important limiting factor in the photoperiodic reaction under greenhouse conditions during the winter months, especially in high latitudes. It should be added that light intensity may be expected to have its greatest effect on photoperiodic induction near the critical day length because of the state of delicate balance between vegetative and reproductive activities created by this photoperiod. It likewise becomes an important factor in the response of short-day plants to very short photoperiods where photosynthesis and nutrition conditions may become limiting and light intensity and light duration function as compensatory factors.

When supplementary illumination is employed only to extend the photoperiod, surprisingly low intensities are effective. For floral initiation in most plants tested, Withrow and Withrow (182) found that an intensity of about 1 foot-candle brought about maximum response. Significant response was noted in spinach and Biloxi soybean with an intensity of 0.1 foot-candle. Intermittent supplementary illumination also was found to be effective but with equal energy values was less so than uninterrupted light. In the long-day plant, *Agrostemma Githago*, Harder and associates (77) found that under some conditions an intensity of only 5 foot-candles as supplementary light gave maximum acceleration in floral induction. Significant effects were obtained with intensities of less than 0.02 foot-candle, which is the intensity of full moonlight. In general practice, however, it seems advisable to employ supplementary illumination intensities of 10 or more foot-candles to insure clear cut results.

It remains to briefly consider the *effective* natural length of day in photoperiodic induction. In dealing with photoperiodic data applying to natural illumination it has been almost universal practice to refer to the "length of day" as the period from sunrise to sunset, although it is well known that some portion of the twilight also contributes to the day-length effect on plants. The maximum intensity of skylight at the beginning of civil twilight in the morning and at its end in the evening is 0.4 foot-candle. At sunrise and sunset the maximum intensity of the light is about 33 foot-candles. The duration of the civil twilight in the morning and in the evening ranges from about 22 minutes at the equator to 32 minutes at 40° latitude. It appears, therefore, that under the most favorable conditions, the effective day length for highly sensitive plants may be at least 40 minutes longer than the period from sunrise to sunset. For less sensitive plants or when the sky is not clear the twilight component of the effective length of day may be much shortened or even completely nullified.

Influence of Wavelength

A great deal of research has been conducted in the relative effectiveness of various regions of the visible spectrum in bringing about photoperiodic induction--one of the principal objectives being to identify the pigment or pigments concerned in the photoreaction participating in the process. Because of the difficulty of obtaining even approximately pure monochromatic radiation having the necessary energy values, most of the work in this field has been based on use of colored light to supplement a basal, relatively short, daily period of natural light. Relative effectiveness of the various wavelengths was measured, of course, by the accelerating action of the lengthened photoperiod on floral induction in long-day plants and inhibiting induction in short-day plants. For the most part, conflicting and puzzling results have been obtained, probably because of lack of adequate purity in the various wavebands used, their excessively low energy values or lack of balance in these energy values.

Working with long-day and short-day types from various latitudes and applying supplementary filtered light of various wavelengths stated to be of equal intensities, Rasumov (142) found that only the red end of the spectrum was effective in controlling floral initiation in all plants tested. There were decided differences between the plants as to light quality requirements for flowering. Long-day plants from high latitudes definitely required red rays but those from lower latitudes were able to utilize short wave light in larger part in the flowering response. In short-day plants maximum fruitfulness was obtained with short wavelength illumination.

Schappelle (147) obtained approximately equal acceleration of reproduction--growth response in several long-day types with red and blue radiation of equal energy value when used as supplemental illumination. In several typical short-day plants both the blue and the red wavelengths were effective in inhibiting flowering. Radiation from each end of the spectrum applied alone produced injury and abnormal growth, the bad effects of the blue end being greater.

Withrow and Biebel (181) found that as supplemental light, blue radiation accelerated flowering of certain long-day plants while red radiation was effective with all of them and green was not fully effective in any case. Several short-day plants remained vegetative under the red rays but flowered under the blue and green. Over a period of 10 years, Funke (52) investigated the effects of supplementary red and blue radiation on flowering in more than 100 species and varieties of plants. The test plants were exposed to open natural light from 7 a.m. to 3 p.m. and to natural light filtered through colored and white glasses during the remainder of the day.

Most plants could be grouped into four classes according to their reactions, as follows: (1) The red light produced the same effect as white light, but the blue produced the same effect as darkness; (2) both the red and the blue gave the same effect as white light; (3) both the red and the blue gave the same effect as darkness; (4) the red gave the effects of darkness and the blue gave the effects of white light. In nearly all cases the comparative effect on longitudinal growth differed from the effect on reproduction. Ball (12) ascertained that with equal energy values the shorter red rays were as effective as white light in inhibiting unfolding of blossoms of Turnera ulmifolia var. elegans that were ready to open, when used to irradiate them at night.

In their researches in this field, Borthwick and associates (19) employed a spectrographic arrangement designed to supply high intensity radiation of adequate purity from any desired, relatively narrow wavelength region of the spectrum. To measure relative effectiveness in floral initiation, use was made of the principle that brief illumination of sufficient intensity applied near the middle of a dark period of about 12 to 14 hours will inhibit photoperiodic induction in short-day plants and stimulate it in long-day plants. For Biloxi soybean and cocklebur a band of wavelengths extending from about 560 to 720 mu in the orange-red proved to be the most effective in inhibiting formation of flower primordia while a narrow band in the violet centering near 400 mu also was rather highly effective. The region around 480 mu in the blue-green was especially weak in action and wavelengths longer than 720 mu, including the infrared, showed no activity. By the same procedure a spectral curve of relative effectiveness was developed for spike formation and stem elongation in a winter barley, a long-day plant, and was found to be similar to the curve obtained for the short-day plants. The same authors, in collaboration with Went (130), next worked out a spectral efficiency curve for leaf elongation in etiolated seedlings (free of chlorophyll) of *Pisum sativum*. The curve obtained, again, was similar to those relating to control of floral initiation.

Nutritional, Metabolic, and Anatomical Relations

Soon after the discovery of photoperiodism, studies were initiated on the chemical changes taking place in plants in connection with the clearly defined growth and developmental effects of photoperiod. A large portion of the earlier biochemical research relating to photoperiodic induction was concerned with the much-discussed carbohydrate-nitrogen ratio as a factor in the transition from the vegetative to the sexually reproductive state in plants.

As a special phase of the general problem, relative photosynthetic activity in typical long-day and short-day plants has received considerable attention. Likewise, several workers have made observations on interrelations of the mineral nutrient supply and length of day in growth and development phenomena. The earlier literature bearing on nutritional factors concerned in photoperiodic induction has been reviewed by Murneek (116) and by Loehwing (99).

Tageeva (160) found no significant relation between photosynthesis and photoperiodic induction in either the oat, a long-day plant, or millet, a short-day plant, grown under long and short photoperiods. Differences in utilization of the assimilate seemed to be the principal cause of differences in accumulation of dry matter in the long-day and short-day plant types grown under the long-day and short-day conditions. Other workers have observed that many plants store carbohydrate in the form of tubers or thickened roots when exposed to a short-day and, obviously, the plants are unable to use the carbohydrate for protein synthesis or other forms of assimilation.

Under the influence of even very weak supplementary light, growth and flowering usually are stimulated and the carbohydrate promptly comes into use in support of these processes. The more typical short-day plants, moreover, normally enter the reproductive phase when exposed to a short day, even though the total production of carbohydrate is sharply reduced (136). Claes and Melchers (36) were unable to confirm the suggestion of Grainger that inhibition of floral initiation in short-day plants by exposure to long day may be due to lack of adequate translocation of carbohydrate from the leaves to the growing points during the short night. It was found, instead, that light did not interfere with mobilization of carbohydrate in either a short-day strain or a day-neutral strain of Xanthium.

Several investigators (16, 31, 61) have observed that in various plant species and varieties, exposure to short photoperiod causes an initial decrease in content of chlorophyll but after 2 weeks or longer the content rises well above that applying to growth under long photoperiod. In the early research bearing on the relation of the carbohydrate-nitrogen (C/N) ratio to photoperiodic induction, perhaps the most comprehensive studies were those of Arthur et al. (9) on many plant species grown under accurately controlled conditions and exposed to various photoperiods. Chemical analyses made at several stages of growth showed in some species a relatively narrow change in the C/N ratio under a wide range in photoperiods, while in others there were marked changes. There was no definite relation between content of carbohydrate and nitrogen and initiation of flowering in either short-day plants or the long-day type.

In studies with tuber-forming species grown in long and short photoperiods, Tincker (165) observed that a deficient supply of potassium slowed down somewhat the translocation of carbohydrate to the underground storage organs in the plants given short photoperiod. The rate of accumulation of dry matter in the tubers and roots was controlled primarily by photoperiod. Warington (171), in a study of the influence of length of day on the response of plants to boron, found that exposure to short photoperiod tends to delay the appearance of boron deficiency symptoms, but the photoperiod has no specific bearing on the need of the plant for boron.

In cultures of Marchantia polymorpha L. in a great variety of nutrient solutions, Voth and Hamner (169) found that, independently of the variations in supply of mineral nutrients, differences in photoperiod produced marked effects on growth and development. Vegetative growth and production of gametangiophores were greater under an 18-hour photoperiod but a greater number of gemmae cups were produced under a 9-hour photoperiod. In studies with both short-day and long-day types of plants, Cajlachjan (34) concluded that mineral nutrition conditions do not govern the transition from the vegetative to the reproductive condition. In agreement with Murneek (116), Cajlachjan considered that, contrary to the conclusions of many earlier workers, a liberal supply of nitrogen tends to promote free-flowering and fruiting in many plants. Likewise, Parker and Borthwick (126) were unable to find any definite causal relationship between the plant content of mineral or other constituents and floral initiation in Biloxi soybeans.

Naylor (121) observed that differences in supply of nitrogen, phosphorus, or potassium affected the rate of development of terminal inflorescences in Xanthium only when the plants were exposed to photoperiods near the critical. Plants low in nitrogen, phosphorus, and potassium had the same critical photoperiod as those amply supplied with these elements. It appears that once the plant has definitely passed from the vegetative into the reproductive condition, the reproductive structures are able to mobilize all necessary nutrients and exercise a large measure of control over growth and metabolism. It was shown by Murneek (116) that in Biloxi soybean under short-day conditions accumulation of carbohydrate and increase in the carbohydrate-nitrogen ratio did not take place until photoperiodic induction had been completed and came about as a result of inhibition of growth.

Harder and Witsch (79) made a detailed study of the very striking effects of photoperiod on succulence in Kalenchoe blossfeldiana, a pronounced short-day plant. The effects on succulence are associated with marked influence of the light period on flowering and the general morphology of the plant. Under long-day conditions the leaves have long petioles, develop a large area with concave upper surface, stand in a horizontal position and are weakly succulent. The leaf pairs are separated by long internodes. Under a 9-hour daily light period the leaves are very small, apetiolate, turgid, very strongly succulent, and form an erect-standing basal rosette. The leaves produced under the short photoperiod are extraordinarily thick and sappy. This unusual thickening of the short-day leaves is due to increase in volume rather than increase in number of the mesophyll cells. Along with the morphological modifications, the short day also causes physiological changes, which greatly alter the water economy of the plant. The succulent type of plant produced by short photoperiod is highly resistant to drought while the long-photoperiod type is quite sensitive to a reduced water supply. Thus, cut leaves of plants grown in long photoperiod lost one-half of their water content in 2 days, but corresponding leaves of plants grown with short photoperiod retained more than 50 percent of their water at the end of 3 weeks. The authors concluded that the two phenomena of flower formation and succulence, which are stimulated by short photoperiod, apparently are not controlled by the same mechanism. In contrast with Kalenchoe, several species of Sempervivum, which are long-day plants, develop a considerably increased degree of succulence when growing in long photoperiod (13).

The influence of photoperiod on the anatomy of the axis and other plant organs has been considered by many investigators. Deats (41) found that in tomato and black pepper stems the amounts of both phloem and xylem and the thickness of their cell walls increased with increase in photoperiod. Struckmeyer and Roberts (158) observed that in a large number of species studied, marked reduction in cambial activity and corresponding decrease in phloem formation take place consistently as the plants pass into the reproductive state in response to photoperiod or other favorable factors of the environment. Withrow (178) reported similar observations.

Temperature Interrelations

The interrelation of temperature and photoperiod in plant growth and development has received much attention, especially in connection with the extensive research that has been conducted in vernalization since about 1932.

A large portion of the work in this general field, however, relates essentially to the effects of temperature as such, without close relationship to the photoperiod and therefore does not come within the scope of the present discussion. With respect to the more direct influence of the temperature on photoperiodic induction, it appears that the relation is more or less in line with the principles laid down by Sachs, covering the temperature requirements of plants at various stages of development. Within the range to which a particular species is adapted with respect to sexual reproduction, decrease in temperature below the optimum may be expected to increasingly delay flowering in response to a given photoperiod, as the minimum temperature for this phase of plant development is approached (106, 155).

In some instances low temperature has the effect of shifting the critical photoperiod of long-day plants to a lower level (95) but in certain other plants of the long-day type high temperature seems to have a more or less similar effect (117). Briefly, when compared over a sufficiently wide range in temperature, some species and varieties tend to behave as day-neutral types, whereas, under a narrower temperature range, they would normally be classed as short-day or long-day plants. Again, these temperature effects on photoperiodic expression seem to be in line with the concept of Sachs. On the other hand, varieties or strains within a species, which differ markedly with respect to critical photoperiod may exhibit only limited and more or less similar rates of acceleration or retardation in photoperiodic response when subjected to temperature differences covering a comparatively wide range, as is true of soybean (155). For example, the three varieties, Mandarin, Peking, and Biloxi, flower readily at a fixed temperature as high as 89° F., when exposed to photoperiods of 6 to 12 hours. As shown in figure 6, there is no significant selective or differentiating action of temperature on these varieties through the range 71° to 89° F. In a low night temperature (55°), however, the number of flower primordia formed in photoperiodic induction was decidedly smaller than in a temperature of 65° F. or higher (127).

In view of the sharply contrasted characteristics of the photoperiodic action curves of the more typical short-day and long-day plants (fig. 4), a true reversal of photoperiodic response in either plant type arising from temperature difference would seem to be quite unlikely.

The typical effects of chilling the germinating seeds (vernalization) on the photoperiodic responses of the resultant plants may be illustrated by the results obtained in a study of this problem by Purvis (137). When the seed of a typical winter rye were germinated at 1° C., the formation of flower primordia as well as stem elongation and ear emergence were stimulated by the natural long day. After germination at 18° C. on the other hand, floral initiation was accelerated and appreciably intensified by a 10-hour day, while a long day was required subsequently for even comparatively slow elongation of stems and emergence of ears. Thus, pretreatment with short days brought about essentially the same result as chilling during the germination period, namely, causing the treated plants to exhibit the characteristic rapid response of the spring cereals to long day and warm temperature. Although most plants responding to vernalization are thereby caused to behave as typical long-day plants, Harder and Denffer (76) found that Sinapis alba responded best to chilling of the germinating seed, with respect to flowering, when grown under short-day conditions.

It remains to direct attention to unfavorable effects on floral induction that may result from a combination of very short days and warm temperature in heated greenhouses during the winter months in high latitudes. Under these conditions consumption of carbohydrate in respiratory activity is likely to exceed the gain from photosynthesis so that flowering may be inhibited even though the prevailing photoperiod under other circumstances would induce floral initiation. Since the green parts of the plant, especially foliage leaves, tend to be at least self-supporting with respect to carbohydrate supply, their growth would not be as readily affected by the relatively low rate of carbon fixation.

Mechanism of Photoperiodic Induction

Extensive research has been conducted on various aspects of the physiology of flowering in angiosperms in which appropriate photoperiods have been employed to control floral initiation and the succeeding phases of sexual reproduction. In general, the immediate objective has been clarification of numerous aspects of the mechanism underlying photoperiodic induction. That photoperiodic response may be localized in the plant by appropriate use of contrasted light periods was demonstrated by Garner and Allard (62), who found that when the apex of Cosmos sulphureus, a short-day plant, was maintained in continuous darkness while the branches were exposed to short photoperiod, flowering subsequently took place in the apex when exposed to long photoperiod. These tests were greatly extended by Knott (89), Cajlachjan (32), Moshkov (114), and others and the results have clearly indicated that in both the long-day and the short-day plant types the fully expanded foliage leaves perceive the photoperiodic stimulus which, in due course, must be transmitted to the meristems in order to bring about floral initiation. This finding furnished in part the basis for development of the much discussed theory that photoperiodic induction involves the synthesis and action of a specific flower-forming hormone. It has been pointed out by several commentators that this theory is but a revival of Sach's concept of long ago that plants produce specific "organ-forming substances" in their leaves that are capable of regulating development.

Since the hypothetical flower-forming hormone has not been isolated and chemically identified all evidence as to its existence is indirect. This evidence relates largely to conditions applying to effective transfer of the reproductive stimulus from the leaves to the meristems of the same or another plant, as evidenced by the responses of the latter under a great variety of treatments. In addition to numerous modifications of the localization experiments previously referred to, in combination with various defoliation procedures, extensive studies in grafting were made to obtain more convincing evidence that transfer of the flowering stimulus from the leaf to the growing points is by means of a material substance moving through the intervening plant tissues in relatively minute quantity (33, 53, 71, 72, 93, 108, 109, 114).

Cajlachjan proposed the name "Florigen", for this substance. The results of these extensive studies, as a whole, indicate that movement of the stimulant or hormone is through the living tissues and takes place at a slow rate but with approximately equal readiness upward, downward or transversely in the stem. In some instances it has been observed that transmission of the stimulus in short-day plants from a stem exposed to short day to another branch exposed to long day is more or less inhibited if the fully expanded leaves of the receptor branch are allowed to remain but it appears that there are exceptions to this type of reaction (51). The hormone or stimulus passes across graft unions without difficulty and by this means has been successfully transmitted from short-day to long-day plants in either direction and from annuals to biennials, suggesting that but a single flowering hormone is concerned in floral initiation, irrespective of genotype or photoperiodic class.

It has been suggested by some investigators that plant growth regulators rather than a specific flower-forming hormone may be concerned in the transmission of the flowering stimulus from the leaves to other plant parts. However, it was found by Cajlachjan and Zdanova (35) that in long-day, short-day, and day-neutral plants alike, the auxin content of the upper part of the stem increased with increase in the length of the day to which the plants were exposed, regardless of whether flowering took place, while the full grown leaves contained no auxin. Again, when the seed of numerous species and varieties were soaked with indoleacetic acid solutions of various concentrations before planting, in no case was flowering directly affected in seedlings.

A question of special interest concerning short-day plants has been whether photoperiodic induction is controlled by the length of the photoperiod or the length of the dark period. The evidence clearly indicates that in some, and probably in all, short-day plants, floral initiation is conditioned by the duration of both the light period and the dark period of the cycle (18, 71, 106). Hamner (72) suggested that in the short-day plants certain reactions essential to induction take place only during the light period while other equally necessary reactions take place during the dark period. It is assumed, further, that there is action between the light-activated and the dark processes which provides the medium for the observed induction effects. Harder and associated (78) proposed an interpretation of the photoperiodic reaction in short-day plants which differs somewhat from Hamner's hypothesis with respect to the dark reaction involved. Originally these reactions were considered to be influenced by the intermediate products of photosynthesis but their more recent results have caused these authors to question the significance of photosynthesis to the dark processes.

Since floral initiation takes place in long-day plants exposed to continuous light, it seems that the only effect of the daily dark period under natural conditions is to retard or to inhibit the reproductive processes. Lang and Melchers (95) found that in the annual form of Hyocyamus niger, a long-day plant, flower formation does not take place under short photoperiod because of inhibiting processes localized in the unfolded leaves. When the plants were defoliated, flower formation took place independently of the photoperiod while grafting even a single leaf to the stem restored the sensitivity to short day. It was concluded that inhibition of flowering under short photoperiod is due essentially to dissimilation processes taking place during the corresponding long dark period, since introduction of sugars into the leaves removed the inhibiting action. Whether similar relations apply to other long-day plants apparently has not been ascertained.

Bünning (26) stated that floral induction and other features of photoperiodism are linked with an endogenous diurnal rhythm of the higher plants. Of the two phases of the rhythm, one is adjusted to the natural day and the other to the dark period. The light phase is characterized by predominance of synthetic assimilatory processes while the dark phase embraces chiefly processes of a hydrolytic nature and increased respiration. Although fundamentally the inner rhythm is endogenous genotypically, yet under natural conditions the light and dark phases are strongly regulated by the alternation of day and night.

In preceding paragraphs attention was called to certain quantitative aspects of the photoperiodic reaction, all of which seem to be consistent with the hormone theory of flowering and fruiting regulation. It has been emphasized that photoperiods lying near the critical typically produce only a weak flowering stimulus, which usually results in sparse and more or less delayed flowering and fruiting. Further, in certain cases changes took place in near critical photoperiods during the reproductive stage, especially when associated with changing light intensity and may bring about marked abnormalities in the sex organs, including more or less complete sex reversal. In this connection mention should be made here of a striking floral abnormality in the form of so-called "vegetative flowers" which are produced in certain plants when subjected to distinctly suboptinal photoperiodic conditions. Presumably this effect is the result of an inadequate supply of the flower hormone for maintaining intensive reproductive activity, since the vegetative flowers can be obtained, for example, by exposing only one or a very few leaves of a short-day plant to a short photoperiod for a limited time while the rest of the plant remains under a long photoperiod. This type of flowering abnormality has been studied in detail by Behrens (13), in Harder's laboratory.

Genetic Relations

Plant breeders have made extensive use of regulated photoperiods for synchronizing flowering in species and varieties for hybridizing purposes and in growing two or more generations of the breeding material within a year (68, 115). The objective involved may relate to better or wider latitudinal adaptation or to properties, such as disease resistance, which are not necessarily associated with photoperiodic response. The genetic aspects of the mechanism of photoperiodism do not seem to have received the attention that the importance of the subject merits, either by physiologists in connection with their study of the photoperiodic reaction or by geneticists from their own point of view.

The frequent occurrence within a plant species of varieties and strains that differ sharply in their photoperiodic requirements has been mentioned repeatedly. Close control of genetic purity in such material with respect to sensitivity to photoperiod may present difficulties because of lack of distinguishing morphological differences. Obviously in such circumstances ordinary methods of seed selection cannot be relied upon for developing photoperiodically pure lines. There is also the possibility that photoperiodic mutations will appear. This situation tends to render somewhat uncertain the interpretation of results based on quantitative data or observations covering only a few individuals.

A limited number of investigations have been conducted on the mode of inheritance of the photoperiodic reaction in both long-day and short-day plants. Before the discovery of photoperiodism, Allard (2) found that the property of not flowering exhibited by the Maryland Mammoth variety of tobacco when grown during the summer, acted as a recessive character in crosses with ordinary Maryland tobacco (*N. tabacum*), a day-neutral type.

Lang (94) made a study of the inheritance of the short-day character in the Maryland Mammoth variety when crossed with the "Java", a commercial form of *N. tabacum* of day-neutral or very weak long-day characteristics. It was concluded that the short-day character is dependent upon a single gene and is recessive, although dominance of the day-neutral character probably is incomplete. The factor controlling flowering likewise influences branching and stem height. Lang believed that appearance of short-day forms similar to the Maryland Mammoth, as single-gene mutations is of comparatively frequent occurrence in *Nicotiana tabacum*. Little and associates (97) obtained similar results in *Tagetes*. In crosses of winter and spring forms of *Lactuca sativa*, which are long-day types, with the summer forms, which are day-neutral, Bremer and Grana (23) found that the long-day character was dominant and governed by a single factor. However, in an investigation of inheritance of differences in seasonal time of flowering in three short-day strains of *Solidago sempervirens*, Goodwin (68) concluded from an analysis of the F_1 and F_2 hybrid populations that a large number of genes are concerned. A question of major interest in this field would be the inheritance of seasonal differences in flowering time in hybrids of pronounced long-day and short-day types. Unfortunately both of these types rarely, if ever, occur in the same species. Lang (104) found that experimentally produced autotetraploids of long-day, short-day and day-neutral types studied by him did not differ greatly in their photoperiodic behavior from the diploid parent forms.

Horticultural and Agronomic Applications

By suitable control of the daily illumination period, most plants of horticultural and agronomic interest can be caused to flower and fruit at any time during the year, provided they are grown in an environment reasonably well suited to their needs in other respects. Moreover, by regulating in this way the duration of the vegetative phase of growth, the size attained by the plants can be greatly modified. To accomplish these results it is only necessary to shorten the natural daylight period or to lengthen it according to the latitude, the time of year at which the response is desired and the specific photoperiodic requirements of the plants dealt with. The relatively simple methods previously outlined can be employed in darkening the plants or giving them supplemental illumination in the greenhouse or in the open. In tropical and subtropical regions the treatments usually can be applied at any season of the year.

At intermediate latitudes greenhouses usually will be required during the winter season and at very high latitudes culture in the winter season will be restricted because the very short days and relatively low light intensities oftentimes will not provide adequate photosynthesis. With sufficient intensity and duration of daylight to provide basal nutritional needs, supplemental illumination usually can be provided at low cost, since intensities of 10-foot candles or even less frequently are adequate.

Typical short-day plants such as the Christmas poinsettia and late forms of chrysanthemum are easily brought into flower in midsummer or at any desired intervening date by shortening the photoperiod to about 10 hours. In the same way, by the use of supplemental light for a few hours after sunset, many summer-flowering plants can be forced into bloom in the fall, midwinter, or early spring, provided the basal illumination is adequate. Of course, flowering in either plant type can be delayed as long as may be desired by applying photoperiods which inhibit the process. Again, by properly combining the photoperiodic effect with the accelerating or retarding effects of suitable temperatures, accurate timing of anthesis for such occasions as Christmas or Easter is possible. Considerable experimentation has been carried out in this field and specific recommendations have been developed for control of flowering in various plants (131, 135). Where artificial control of photoperiod is not practicable and time of flowering and fruiting is not a major consideration, date of planting in relation to natural day length may be of considerable importance with respect to yield.

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